IDENTIFYING MECHANISMS OF PERSISTENCE FOR GROUND LIZARDS (REPTILIA: AMEIVA) IN THE CARIBBEAN INFORMED BY HABITAT, PHYSIOLOGY, AND PREDATION

A Dissertation

by

NICOLE FRANCES ANGELI

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Chair of Committee,	Lee A. Fitzgerald
Committee Members,	Thomas Lacher
	Donald Miles
	Lisa Ellis
Head of Department,	Michael Masser

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ABSTRACT

Understanding what allows species to persist is a complex challenge for biodiversity conservation. Biophysical constraints on habitat use and predator evasion can affect the persistence of at-risk species. To study persistence of species threatened by invasive predators, I integrated 1) field surveys to quantify the habitat use of a lizard species (*Ameiva polops*) that is rare across its landscape due to predation pressure; 2) habitat models to identify suitable habitat for the same rare species; and 3) physiological trials to determine if the widespread persistence of a closely-related lizard species (*Ameiva exsul*) where predators occur is aided by shifts in its thermal ecology. Multiple datasets generated from my dissertation included field surveys, population demographic models, and physiological datasets. By incorporating fine-scale physiological data into population abundance models, I found that temperature was important for rare and widespread lizards in the genus *Ameiva.* I estimated occupancy and abundance of *Ameiva polops* incorporating thermal landscapes (Chapter II). Evaluating the landscape of threats on St. Croix, we find that *Ameiva polops* may be repatriated to parts of its historic range despite existing threats at broader scales (Chapter III). Last, where widespread species *Ameiva exsul* co-occurs with mongoose predators, individual lizards have population-level increases in upper thermoregulatory temperatures (Chapter IV). As a student in the Applied Biodiversity Science Program, I worked with local actors and institutions to implement and promote conservation actions related to these findings.

DEDICATION

This dissertation is dedicated to conservation managers, who do more with less every day; volunteers, who make conservation action possible; and their families and friends. Conservation practitioners inspire me to harness the ideas within the academy to benefit a world rapidly changing outside the ivory tower.

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In closing, I celebrated the conclusion of my Smithsonian Predoctoral Fellowship with a duck feast in Chinatown with the Kevin de Queiroz lab. The end-of-dinner fortune cookie read cheekily, 'The only thing we know for sure about future developments is that they will develop'. I agree: we live in a changing world, and our science is changing the world. While we may never know the precise how, why, or what causes all species to persist, we can always strive to do a little better in aiding their survival. This dissertation and the people acknowledged here support that idea. Any omissions are my fault entirely, and I deeply apologize!

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CHAPTER I

INTRODUCTION

Anthropogenic changes to landscapes are more rapid today than ever (Purvis et al. 2000), and many species require human interventions and adaptation strategies to survive (Germano et al. 2015). A complex question that is still largely unanswered is why some species survive, while other closely related species go extinct. These two responses, persistence and declines, may be buffered by life history and physiological traits (Sinervo et al. 2010, Parmesan et al. 2006). Recent studies suggest multiple components, like predation risk and thermal tolerance, interact in concert to affect species survival (Doherty et al. 2015, Bastille-Rousseau et al. 2016b, Bennett et al. 2015). The integration of disparate lines of evidence to understand mechanisms of species survival was my primary research goal for this dissertation. To disentangle the roles of predation risk, thermal tolerance, and land use on the persistence of species, my approach depended on integration of findings from 1) field surveys to quantify animal abundance across landscapes, 2) spatially explicit models to describe the effect of thermoregulatory preferences of species on their distribution across the landscape, and, 3) physiological experiments to quantify thermal trait variance within and among species. Taken together, my research explored how an integrated understanding of functional traits of species, biotic interactions with predators, and patterns of land use determine the ability of species to persist in complex landscapes.

My work took place in the Caribbean, a biodiversity hotspot with endemic and native species under intense pressures from introduced exotic predators, climate change,

and habitat loss (Crother 1999). Management of at-risk species in the Caribbean has generally focused on developing strategies to protect charismatic animals and fisheries including sea turtles, marine mammals, endemic iguanas, and parrots during critical life stages. Yet the pressures in the Caribbean occur for all taxa, including amphibians (Young et al. 2005), reptiles (Fitzgerald et al. 2017), and birds (Blackburn et al. 2004). Finding new solutions immediately applicable to conservation of Caribbean fauna is an on-going conservation challenge. For example, many native species declined or went extinct in the Caribbean where the Small Indian Mongoose (*Herpestes auropunctatus)* was introduced for biocontrol of black rats and roof rats that were pests on sugar cane crops (Lewis et al. 2011, Barun et al. 2013, Seaman 1952). Public and private mongoose control programs now exist in almost all Caribbean nations in an attempt to reduce predation pressure from mongoose on native species. However, fewer than half of sixty reported programs have demonstrated any reduction in mongoose numbers, and eradication was achieved only on islands smaller than 115 ha in size (Barun et al. 2011). One affected species, the St. Croix ground lizard *Ameiva polops* Cope, 1862 (Sauria: Teiidae) remains vulnerable despite being listed as Endangered under the U.S. Endangered Species Act for 30 years, and with more than 50 years of conservation actions facilitated by the U.S. Fish and Wildlife Service, the National Park Service, Texas A&M University, St. Croix Environmental Association, and the U.S. Virgin Islands Department of Planning and Natural Resources. The species has persisted on four small offshore islands comprising less than 1% of its historic range (Fitzgerald et al. 2015). The St. Croix ground lizard and other Caribbean species in recovery stasis need

new ideas for their conservation that are immediately applicable in human-modified landscapes. Otherwise, species like the St. Croix ground lizard that are susceptible to mongoose predation will be destined to live in small vulnerable populations in perpetuity, or until they go extinct by stochastic events.

The Puerto Rican land bank, an archipelago of more than 175 islands, was united just 13,000 years ago during the last glacial maximum, creating a study system with a common geologic and evolutionary history with potential for comparing how populations within and among species respond to threats. Within the general area of the Puerto Rican land bank, the ground lizard genus *Ameiva* includes three species in one phylogenetic group (Tucker et al. 2016). Closely related genera include an additional 18 species of ground lizards. I focused my research on two of these: a persistent species, (1) the widespread *A. exsul* found commonly on more than 67 islands*;* and, (2) a declining species, the endangered *A. polops,* with individuals on just four small cays (Hurtado et al. 2012). Most of the Puerto Rican land bank and St. Croix experienced ~90% forest loss from 1750 to present, with those lands converted to agricultural use (Brown and Lugo 1990, Crother 1999). Mongoose predation precipitated widespread extinctions and declines of native fauna after introductions to Puerto Rico in 1877 and to St. Croix in 1884 (Barun et al. 2011, Hoagland et al. 1989, Horst et al. 2001). Mongoose caused the extirpation of other species, including the loss of the St Croix ground lizard from the main island, which comprised more than 99% of its historic range (Philibosian and Ruibal 1971). In contrast, the Puerto Rican ground lizard persisted and continues to co-exist with mongooses across much of its range (Henderson 1992). In this dissertation, I

asked if the decline of one but not both species of ground lizards is enigmatic or a consequence of each species' biology and aspects of the environment.

In the second chapter, I built a mechanistic model to describe abundance of the St. Croix ground lizard (*Ameiva polops)* on one of the islands where it occurs. Mechanistic models require in-depth knowledge of individual species (Buckley 2010). Thus, I created a landscape dataset of thermally suitable area to identify where the lizards may disperse. Biological traits act synergistically with environmental conditions (Brook et al. 2008, Pyšek et al. 2012, Chevin et al. 2010), so I also quantified environmental gradients useful in characterizing aspects of the St. Croix ground lizards' occurrence, distributions, and dispersal (Buckley 2010).

In the third chapter, I used physiologically-informed habitat associations of the St. Croix ground lizard to identify areas where it could be reintroduced to its historic range. Identifying suitable regions for repatriation requires integrating multiple lines of evidence including governance, threats, resources, and habitat (McDonald and Boucher 2011). Landscape designs that exclude non-native mammalian predators from peninsulas, sanctuaries, and offshore islands are increasingly common. The New Zealand Predator-Free Initiative is approaching the challenge of repatriation of its lost fauna similarly, hoping to scale repatriation from refuges to entire landscapes (Norton et al. 2016, Pech and Maitland 2016, Russell et al. 2015). I predicted that landscapes have emerged in the post-agricultural era on St. Croix to contain significant amounts of suitable habitat for the St. Croix ground lizard and refuge from mongooses.

In the fourth chapter, I measured physiological traits of Puerto Rican ground lizards in the laboratory to explore differences that may explain their coexistence with mongooses. In the lizard family *Teiidae*, thermoregulatory behaviors play a strong role in determining distributional and demographic status (Huey and Kingsolver 1989). Thermal breadth in a congeneric mainland species, *Ameiva festiva*, was greater in the laboratory than what was observed in the wild, which may indicate that rare events impact its survival (Van Berkum et al. 1986). I studied individuals from populations first exposed to mongooses 125 years ago and individuals in populations that are still naïve to mongooses. I sought to determine if thermoregulatory traits are an aspect of lizard biology that can change across populations by favoring survival of individuals exposed to stress. The persistence of ground lizards may be determined by their ability to adapt to landscape-level threats.

Using existing and new knowledge and working with managers to implement conservation action was an important component of these dissertation. Not only are the spatial models I generated used by staff at National Parks and Wildlife Refuges to evaluate sites for herbicide applications and write environmental impact assessments, but also in November 2014, I co-led an inter-agency working group in St. Croix, VI to discuss conservation actions for an endangered species. These actions run across stakeholders in conservation—academics, institutions, and citizens, namely the components that comprise the three-fold foundation of my graduate program in Applied Biodiversity Sciences (Fitzgerald and Stronza, 2009).

Finally, this dissertation was designed to increase our knowledge of how to help

species persist when threats exist and evolve in unexpected ways. I worked with the U.S.V.I. Division of Fish and Wildlife, the U.S. Fish and Wildlife Service, U.S. National Park Service, and other local stakeholders to develop this work into a set of recommendations to help the St. Croix ground lizard recover its historic range and increase to self-sustaining levels. Our world is changing largely due to human action. Human action will be required to reverse, slow down, and stay extinctions and to help species persist in a changing world.

CHAPTER II

POPULATION STATE OF AN ENDANGERED LIZARD ON A SMALL ISLAND[1]

Introduction

Despite the natural utility of population size as a fundamental unit of ecological analysis (Elton 1927, Joseph et al. 2006, Krebs 2014), estimating population size is difficult. Abundance and detection of species vary with environmental heterogeneity, for example as habitat transitions, species interact, and landscapes change (Meot et al. 1998, Watson et al. 2004, Mackenzie et al. 2006, Rodda et al. 2015). Thus, mathematical models have been developed to account for biases created by abundance and detection probability (Royle 2004, Royle and Dorazio 2008). Here, we specifically use the *N*-mixture model, which is a method used to estimate latent abundance by accounting for imperfect detection through comparison with mathematical distributions (Kéry and Royle 2010, Knape and Korner-Nievergelt 2016). To date, *N*-mixture models have described basic changes in populations varying along environmental and biological gradients when detection is imperfect (Royle and Nichols 2003). For example, *N*-mixture models have revealed effects of hiking trails on salamanders (Milanovich et al. 2015), drought on alligators (Waddle et al. 2015), and localized competition between native and invasive geckos (Buckland et al. 2014). Here, we use an *N*-mixture model to determine the successful establishment of a population of the endangered St. Croix

[1] Reprinted with permission from "Dispersal and population state of an endangered island lizard following a conservation translocation" by Angeli NF, Lundgren IF, Pollock C, Hillis-Starr Z, Fitzgerald LA. 2017. *Ecological Applications,* In Press.

ground lizard (*Ameiva polops)* five years after a conservation introduction (translocation outside the native range; Seddon et al. 2012, Fitzgerald et al. 2015). We developed a five-step process to account for relevant species' biological traits that can be applied to dispersing populations when detection is less than perfect.

Available habitat is a critical factor mediating the dispersal dynamics of new populations, and of particular importance when identifying appropriate sites for conservation introductions. Landscape configuration affects the distribution of temperatures in microhabitats where ectothermic animals move, forage and interact (Huey et al. 2009). Temperatures existing within available habitat are commonly measured by a heat transfer metric called the operative environmental temperature. The operative environmental temperature is an index of potential heat transfer between ectotherms and their environment measured by thermometers that are calibrated to live, individual animals or calculated with heat transfer equations (Dzialowski 2005). The distribution of operative temperatures across a landscape can be thought of as a physiological index for potential activity and habitat suitability, providing a biological basis for understanding variation in the relative abundance of animals (Sears and Angilletta 2015). In a modeling framework, operative environmental temperature tests whether thermally available habitat affects latent abundance and impacts on detection.

Because *N*-mixture models have the ability to test a range of environmental and biological variables, they bring great potential to the challenges of monitoring spreading populations (Mazzerolle et al. 2007). For both native species relocated for conservation and non-native species introduced accidentally, initial locality is often known.

Spatiotemporal gradients, which characterize expanding populations as individuals radiate from an introduction locality, last until an equilibrium state has been reached across the available region (Bled et al. 2013). Incorporating dispersal gradients into an *N*-mixture model explicitly allows estimation of the spread in addition to true abundance of introduced species (Boulangeat et al. 2012). Dynamic occupancy models are emerging using these techniques (Bastille-Rousseau et al. 2016a). Historically, however, relative abundance models, for e.g., autologistic and linear regressions, used a variety of simple and complex distance metrics to address dispersal (Verboom et al. 1991). Commonly, nearest-neighbor occupancy was quantified as a binary variable with accompanying data, for example, Euclidean distance (Williams et al. 2008). By incorporating dispersal as a covariate corrects the *N*-mixture model for effects of bias towards the introduction locality. The expected result of including mechanisms to understand population abundance is improved occupancy and abundance estimates (Joseph et al. 2006).

With the information to account for spatial heterogeneity and dispersal, a robust number of surveys are completed to count *observed* abundance within sites (Mackenzie et al. 2006). To arrive at *true* abundance within each site, we use the *N*-mixture model, to represent the population state at the present time step. For established populations, modeled abundance also represents the population state at the present time step. The abundance model could also reflect abundance throughout its range, for example, the range-wide abundance of Island Scrub-Jays across Santa Cruz Island, CA was generated using *N*-mixture model parameters (Sillett et al. 2012). In the case of a new population

that is spreading, a dispersal-corrected *N*-mixture model could be fitted across the landscape, but it would estimate the future, post-dispersal population state rather than the present population state. We believe that a dispersal-corrected binomial *N*-mixture model is useful in creating hypotheses for future occupancy and abundance of translocated species and interpolation between sites can achieve that goal (Dickinson et al. 2001).

Our goal was to determine the population size of the endangered St. Croix ground lizard, translocated in 2008 to an island refuge offshore of St. Croix, U.S. Virgin Islands (Fitzgerald et al. 2015). In addition to providing important information on the population state of the critically endangered St. Croix ground lizard, we provide a process to estimate the population state of a dispersing population that has more general application to the problem of estimating the abundance of introduced species while they are spreading. For example our methodology may work to estimate population growth and spread of invasive species (e.g., boas in Florida), and could have applicability to estimating populations of animals carrying disease (e.g., salamander *Bsal*).

Methods

Study species

The St. Croix ground lizard (*Ameiva polops* Cope 1863), endemic to St. Croix, U.S. Virgin Islands was extirpated from the main island due to mongoose predation, which became established on St. Croix in 1884 (Seaman and Randall 1962, Philibosian and Ruibal 1971). Small populations of the St. Croix ground lizard persisted offshore of St. Croix on 1.2 ha Protestant Cay and 5.2 ha Green Cay, and introduced to a 7.5 ha

dredge-spoil island Ruth Cay in 1990 (Hurtado et al. 2012). Fifty-seven animals from the Green Cay population were introduced to 71 ha Buck Island in 2008 and began reproducing almost immediately, and a new population was successfully established on that island (Fitzgerald et al. 2015). Multiple population surveys have taken place to assess the four populations since it was listed as Endangered under the U.S. Endangered Species Act in 1977 (Appendix A).

The St. Croix ground lizard is a small, sexually dimorphic lizard that shuttles between the sun and shade to thermoregulate in the middle of the day and is at other times in one of many underground burrows (Fitzgerald et al. 2015). The maximum snout to vent length of adult males is 95 mm and females reach 65 mm. These active-foraging lizards inhabit relatively dry scrubland on Green Cay, sandy mangrove flats on Ruth Cay, and semi-native landscaped gardens on Protestant Cay (Philibosian and Yntema 1976). Previous habitat assessments indicate that the lizards prefer areas with deep leaf litter, herbaceous ground cover, woody stems which may break up the soil and create space for burrows, loose soils, and sun patches (Moser et al. 2010). Buck Island has undergone forty years of native habitat restoration based on historic pollen records to restore Caribbean coastal forest, scrubland, woodland, manchineel forest, and sandy beaches (Moser et al. 2010, Witmer and Hillis-Starr 2002).

Surveys

We conducted surveys to quantify dispersal of the St. Croix ground lizard on Buck Island in May 2013, May 2014, October 2014, May 2015, and October 2015 for a total of five separate seasons. All 63 sites were surveyed five times during each season

using a visual encounter method, where surveys were terminated after 20 minutes (Rodda et al. 2005). The sites were distributed throughout the entire island and randomly located using ArcGis 10.1 (ESRI) stratified by habitat type (Moser et al. 2010). To ensure independence of surveys, we constrained circular 40 m diameter sites (1260 m^2) to occur at least 80 m apart based on information on the home range $\bar{x}$ = 190 m^2 of the animals from the source population on Green Cay (Meier et al. 1993). Importantly, all surveys at a site were completed within 3 days during a season to eliminate the potential for migration of individuals between sites (Kendall 1999).

During the first season, in May 2013, six observers completed 192 additional abundance surveys at 32 sites on the western half of the island, where we measured dispersal and occupancy on Buck Island during the presence or absence surveys. Individual observers conducted 20 min time-constrained searches for lizards. Each site was surveyed 2 times on a given day, and each site was surveyed on three consecutive days. The first observer walked around a marked circle with a radius of 8 m from the center of the site (50.24 linear m), and a second observer walked around a marked circle with a radius of 15 m from the center of the site (94.2 linear m). They walked in opposing directions. The observers then switched radius and repeated the survey in the counter direction without disclosing information on lizard sightings until the conclusion of all three days. Each survey was used as an independent count to inform the final model. Surveys began at 1130 h, 1230 h, or 1330 h and alternated so that observers surveyed each site in each time period. The timeframe corresponds with the species' peak daily activity from 1000 h to 1600 h (Wiley 1984, Meier et al. 1993).

Covariates

We selected macrohabitat and microhabitat features based on the known associations of the species and included topography and operative environmental temperatures as covariates. We measured microhabitat variables within 1 m^2 quadrats placed in the four cardinal directions approximately 3 m from the center-point of each site and averaged the four data points to acquire a single value in each microhabitat category including: percent herbaceous ground cover on a Braun-Blanquet (1932) index, the number of woody stems > 3 cm in diameter, and average leaf litter depth (cm) of four random points. We calculated the Euclidean distance from the 2008 release area (Fitzgerald et al. 2015) to the survey sites using ArcGis 10.1 (hereafter, distance-from-release). We deployed temperature data-loggers to measure substrate temperature (HOBO Pendant Temperature Logger, Onset Computer Corp, Bourne, MA, USA). We modeled operative environmental temperature with copper models in the shape of lizards, with heads, tails, and legs made from copper foil and tubing measuring 7 cm by 1 cm by 1 cm painted grey (Dzialowski 2005). We placed an iButton© temperature logger inside the lizard model to measure the operative temperature every ten minutes over all 3 days of the survey period. We assigned the average and maximum temperature for the substrate and operative temperature models as covariates in the hour we surveyed the site.

From 30 m^2 remotely sensed data, the elevation was extracted from a digital elevation model (Gesch 2007). We indexed soil types as percent sand, clay, or water in program R (Davis 2002, Debeaudette 2009). The land surface temperature and the

normalized difference vegetation index (NDVI) were derived from Landsat 8 following Weng et al. (2004) and values from the NASA Landsat guide (USGS 2013) in R.

A Multiple Response Permutation Procedure (MRPP) analysis with a Sorensen distance matrix was used to determine if the microhabitat variables we measured within each site homogenously represented the *a priori* habitat types (forest, woodland, shrubland, manchineel, and beach) by repeatedly sorting the sites into the most homogeneous groups. We used two-dimensional nonmetric multidimensional scaling (NMDS) to visualize the habitat variables, and overlaid modeled abundance on the ordinated sites for both the measured and raster variables. We created a convex hull around the sites by habitat type. We reported the fit of the ordination to the observed data matrix as stress, where stress < 0.2 indicated an appropriate fit (McCune and Grace 2002).

Lizard body temperature

We caught and transported ten lizards from Buck Island to mainland St. Croix to measure the preferred temperature and thermal tolerance of the lizards. Animals were allowed to walk freely in a thermal gradient constructed from plywood measuring 4 feet long by ½ foot wide by 3 feet tall. Temperatures in the gradient ranged from 20 °C to 60 °C. Cloacal temperatures of lizards were measured every ten minutes with a K-type thermocouple and digital thermometer. When four consecutive temperature readings within ± 1°C were obtained from the subject we assumed the animal was thermoregulating at its selected preferred temperature (T_{pref}). Thermal tolerance breadth is a standard measure to determine the extreme temperature bounds where animals retain

homeostatic control (Hertz et al. 1993). Cold and heat tolerance trials for each individual were taken after animals achieved their preferred body temperature for at least one hour so that the magnitude of the temperature change did not confound the temperatures at which individuals retained homeostatic control (Angilletta 2009). To measure heat tolerance (critical thermal maximum, *CTmax*), individuals were tethered under a heat lamp until the onset of seizures (Lutterschmidt and Hutchison 1997). To measure cold tolerance (critical thermal minimum, *CTmin*), we exposed animals to cold by placing individuals in a ziplock container and floating each individual in a 5 °C ice bath checking for a righting response when flipped from a ventral to a dorsal position. There was no more than momentary stress for any individual animal and no mortality. The animals were allowed to recover before release the following day at the site of capture on Buck Island.

Occupancy and abundance models

We estimated lizard occupancy across the island using a zero-inflated binomial occupancy model (MacKenzie et al. 2006, Royle and Dorazio 2008). We used habitat type and distance-from-release as covariates in the occupancy model. We ranked models with and without each covariate using Akaike's information criterion (AICc) model selection weight, where the simplest model that best fits the data received the lowest score.

We estimated lizard abundance with an *N*-mixture model using a negative binomial distribution (R package 'unmarked' version 0.10.2, Fiske and Chandler 2011). We fit the null model, which did not include any covariates, and the universal model,

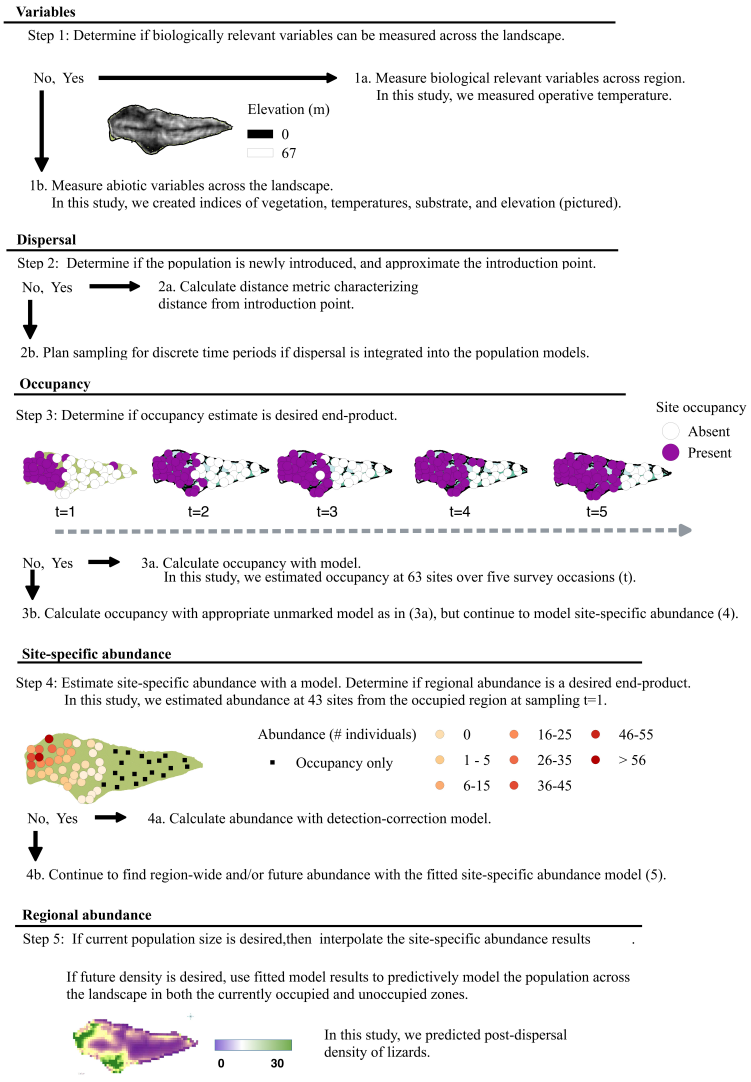
which included all site covariates with the function 'pcount' (Royle 2004). We used stepwise selection to see which environmental variables drove differences in abundance and detection ('MuMIn' version 19.9.5, Barton 2013). We assessed the best models with Akaike's information criterion (AICc), and we used a Wilcoxon rank sum statistic to test the concordance between population estimates from the measured covariates and the raster layers. We used parametric bootstrap sampling (N = 1000 runs) from the function 'parboot' to evaluate the model goodness-of-fit (GOF) using a Freeman-Tukey test statistic, which allows small observed values in the model.

Abundance estimates

To calculate the current population, we exported the abundance site estimates to ArcGis 10.1 and interpolated a surface scaled for root mean square deviation on 30 m^2 grid cells. The 'predict' function in 'unmarked' allowed us to estimate the future abundance state (Kéry et al. 2005). For both the current and future states, we summed the mean abundance and 95 % confidence intervals to arrive at total population estimates.

To present our methods as a step-wise protocol, we created a diagram that summarizes our process (Fig. 1). Five years post-translocation, we collected environmental and biological variables including remotely sensed environmental features, distance-from-release, and operative environmental temperature (Step 1). We measured the population's occupancy across the island over three years to determine if a directional dispersal front characterized the pattern of dispersal in this population (Step 2 – 3). We selected sites within a 100 m buffer of the dispersal front to estimate true

Figure 1. The five-step iterative process used to estimate populations of the St. Croix ground lizard. At each step, a decision can be made to include the data (*Yes*) or to move onto the next step (*No*). If the decision is made to include the data (*Yes*), then the second step (*No*) is included additionally. This approach is amenable for modeling new and dispersing populations.



abundance with a *N*-mixture model in 2013 (Step 4). We estimated the current and future population states by spatially interpolating the modeled abundance between the sites and fitting the binomial *N*-mixture model, respectively (Step 5).

Results

Environmental Covariates

Within all sites, leaf litter depth ranged from 0 to 7.5 cm, woody stems ranged from 0 to 20 per m^2, and canopy covered from 3 to 91 % of the overhead space (Table 1). During the day, substrate temperature ranged from 27.48 °C to 67.50 °C. The operative temperature models at each site ranged from 27.60 °C to 63.50 °C. The mean operative temperature collected at a site within 10 minutes of a lizard observation was 40.30 °C (95 % quartiles: 36.12 °C – 43.36 °C). The NMDS for the measured variables (stress =0.1080) and the raster variables (stress = 0.1130) indicated significant overlap of microhabitat features of Buck Island, thus our *a priori* habitat categories were independent of the microhabitat data that we collected ($R^2 = 0.987$).

Lizard temperature trials

The ten lizard subjects weighed 6.7 g on average (range: 5.4 - 15.7 g). Mean thermal tolerance breadth was 26.08 °C; mean *CTmin* was 19.36 °C (95 % quartile: 17.68 - 21.10 °C) and mean *CTmax* was 45.44 °C (95 % quartile: 45.0 - 46.0 °C). The mean T_{pref} was 39.84 °C (95 % quartile: 39.17 - 40.50 °C). We found that the selected temperatures and heat tolerance of the species fell within the range of available operative environmental temperatures on Buck Island (Fig. 2).

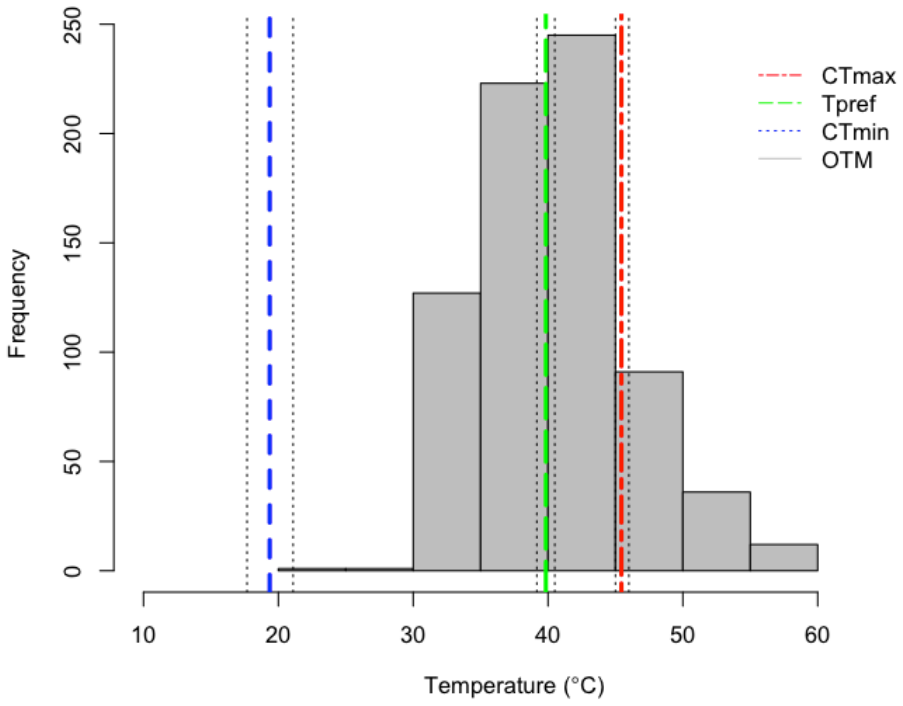
Table 1. Summary statistics for environmental covariates averaged by habitat type on Buck Island. The range for each variable is in parentheses.

	Forest (n=9)	*Shrubland (n=13)*	*Woodland (n=14)*	*All*
Leaf litter depth (cm)	2.12 (0.25 - 6.00)	2.27 (0.13 - 7.50)	1.73 (0.13 - 4.50)	2.03 (0.13 -7.50)
Canopy Cover (%)	40.59 (5.50 - 91.00)	43.44 (14.50 - 73.75)	30.88 (4.50 -48.75)	38.02 (4.50 - 91.00)
Woody stems (#)	6.72 (0.25 - 18.00)	7.79 (0.00 - 20.50)	4.71 (0.75 -13.75)	6.37 (0 -20.5)
Avg. substrate temperature (°C)	28.19 (27.59 - 28.91)	28.93 (27.71 - 30.38)	28.29 (27.48 -29.04)	28.50 (27.48 - 30.38)
Avg. operative temperature (°C)	28.25 (27.60 - 29.31)	28.79 (27.99 - 30.01)	28.56 (27.82 -30.03)	28.57 (27.6 -30.03)

Table 1. Continued

	Forest (n=9)	*Shrubland (n=13)*	*Woodland (n=14)*	*All*
Max. substrate temperature (°C)	49.66 (38.27 - 67.50)	56.26 (42.00 - 67.50)	51.84 (40.5 -62.00)	52.95 (38.27 -67.5)
Max. operative temperature (°C)	52.81 (29.50 - 63.50)	53.10 (47.76 - 62.50)	53.60 (46.00 -62.50)	53.22 (29.5 -63.5)
Elevation (m)	31.31 (2.89 - 67.45)	36.43 (13.70 - 70.10)	35.60 (13.79 -64.65)	34.84 (2.89 -70.1)
Soil moisture (scaled)	1.01 (0.77 – 1.13)	1.04 (0.58 – 1.13)	1.09 (0.86 – 1.13)	1.05 (0.58 – 1.13)
NDVI (scaled)	1.41 (0.24 – 1.83)	1.73 (1.52 – 2.09)	1.73 (1.34 – 2.00)	1.65 (0.24 – 2.09)

Figure 2. St. Croix ground lizard thermal preference (T_{pref}) and heat tolerance (CT_{max}) fell within the range of available operative temperatures (T_{oper}) observed during the survey hours. The cold tolerance limit *(CT_{min})* of the lizard is lower than all recorded operative temperatures during the surveys. Median temperatures of CT_{max}, $T_{pref,}$ and CT_{min} are flanked by range limits (dotted lines).

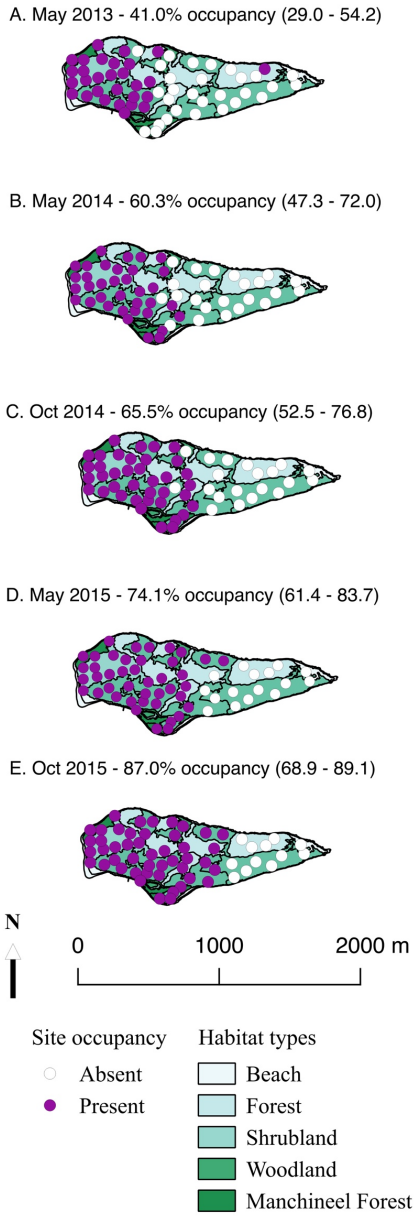


Dispersal and occupancy

Patterns of dispersal across the population were tracked over three years (Fig. 3). In May 2013, we found site occupancy was 41.0 % based on a total of 305 surveys (95 % CI: 29.0 - 54.28 %). From the model, we inferred that observers detected lizards if present at a site 79.7% (95 % CI: 72.1 – 85.6 %) of the time. We only found two lizards on the eastern 47 % of the island (33.3 ha) in May 2013. We found an increasing number of sites occupied with subsequent surveys (Fig. 3). We used these surveys to inform the proportion of sites including a 200 m eastern buffer of absence sites to survey for abundance.

When we re-surveyed the sites in May 2014, we found lizards had dispersed to seven previously unoccupied sites adjacent to sites occupied the previous year. In October 2014, we found three additional sites occupied. Overall, lizards occupied 60.3 % (95 % CI: 47.3 – 72.0 %) and 65.5 % (95% CI: 52.5 – 76.6 %) of the island by May and October 2014, respectively. Detection in 2014 increased from 2013, with observers detecting lizards 94.2 % (95 % CI: 85.6 – 97.8 %) and 86.9 % (95 % CI: 77.9 – 92.6 %) of the time. Lizards had dispersed to four more previously unoccupied sites by May 2015, and an additional four sites by October 2015. Occupancy reached 74.1 % (95 % CI: 61.4 – 83.7 %) and 81 % (95 % CI: 68.9 – 89.1 %) of the island by May and October 2015, respectively. Detection remained high, with observers detecting lizards 96.7 % (95 % CI: 93.3 – 98.4 %) and 97.8 % (95 % CI: 94.9 – 99.1 %) of the time. All years showed good model goodness-of-fit (May 2013 GOF: $P = 0.483$; May 2014 GOF: $P = 0.535$; Oct 2014 GOF: $P = 0.534$; May 2013 GOF: $P = 0.489$; May 2013 GOF: $P = 0.539$). We

Figure 3. St. Croix ground lizard occupancy increased 46 % overall based on annual and biannual surveys conducted from the year 2013 to 2015. Numbers in parentheses indicate 95 % confidence intervals.



did not observe lizards at the far eastern site where we observed two male individuals in May 2013, despite 18 surveys over two years.

Abundance

The May 2013 surveys to estimate lizard abundance in the occupied area included the 32 westernmost sites (presence-absence surveys took place island-wide). Lizard counts ranged from 0 to 18, with an average of 6.3 individuals per site. More than two-thirds (69.15 %) of all lizards we observed were found at sites < 200 m from the 2008 release site (Fig. 4). Observations by the pair of observers were consistent among survey days (First observer: $P = 0.266$, df = 2, $\chi^2 = 2.647$; Second observer: $P = 0.545$, df = 2, $\chi^2 = 1.210$) and between the observers at each site within the survey period ($P = 0.546$, df = 31, $t = 1.23$). Of the individual observations that we made in 2013 during the abundance surveys, we found the majority of lizards observed in full sun ($N = 1{,}322$), with fewer observations of lizards in full shade ($N = 26$) or in partial shade ($N = 92$). We observed most ground lizards under shrubs ($N = 626$), but we also observed lizards among herbaceous vegetation ($N = 220$). Yet, lizard counts varied significantly among sites ($P < 0.0001$, df = 31, $\chi^2 = 189.67$) and by habitat type ($P < 0.0001$, df = 4, $\chi^2 = 29.54$). We observed 16 lizards at the beach site, zero at the manchineel forest site, 167 (per site $\bar{x} = 12.8$, range: 3 - 27) in woodland sites, 42 (per site $\bar{x} = 7$, range: 0 - 19) in forest sites, and 66 (per site $\bar{x} = 3.2$, range: 0 - 13) in shrubland sites.

Abundance Models

We ranked models that allowed only abundance or only detection to vary in order to choose covariates (Appendix B). We found the top abundance model carried 28.1 % of

AICc weights. Factors influencing abundance included average substrate and operative temperatures, maximum operative temperature, distance-from-release, leaf litter depth, percent herbaceous cover, and the number of woody stems (Appendix B; abundance-only top model). The top detection driven model carried 33.7 % of AICc weight. Detection was largely driven by average operative temperature, maximum operative and substrate temperatures, habitat type, percent herbaceous cover, and distance-from-release (Appendix B; detection-only top model).

For the final model, we used the significant covariates from the top abundance and top detection models, and allowed distance-from-release to interact with all layers. This produced a model used to estimate the population size for the entire island (GOF P = 0.636, Table 2). Population estimates based on this model indicated a total of 739 (±27) lizards (95% bootstrap CI: 489 – 1,006) at the surveyed sites. The final model estimated 35 lizards in the recreation/beach site, one lizard at the manchineel forest, 503 lizards ($\bar{x}$ = 38.7, range: 6 - 85 per site) at woodland sites, 128 lizards ($\bar{x}$ = 21.3, range: 0 - 80 per site) in forest, and 140 lizards (per site $\bar{x}$ = 12.7, range: 1- 26) in shrubland sites.

The final model indicated average detection during counts was 20.1 % (CI: 18.5 % -32.1 %). We observed the most lizards near the 2008 release site (maximum of 39 individuals) and < 17 at any site > 125 m from the translocation site. The relationship between distance-from-release and number of lizards observed at sites was statistically

Table 2. The *N*-mixture model used to create current and future population state estimates of St. Croix ground lizards across Buck Island. The contribution and significance of each habitat variable to the abundance of St. Croix ground lizards is indicated by the estimates. The detection model corrects for latent abundance during surveys on Buck Island. See text for details on creating the dataset for the estimation.

	Estimate	*SE*	*z*	*P*
Abundance				
Intercept	-2.16	2.88	-0.75	0.45
Woodland	-0.66	0.22	-3.02	0.00
Shrubland	-0.57	0.35	-1.64	0.10
Manchineel	0.00	5650.00	0.00	1.00
Recreation	-0.01	6260.00	0.00	1.00
Elevation	1.27	0.27	4.70	0.00
Temp	6.27	2.81	2.23	0.03
Dist	0.01	0.01	0.79	0.43
Woodland*Dist	0.00	0.00	1.02	0.31
Shrubland*Dist	0.00	0.00	0.38	0.70
Manchineel*Dist	-0.01	11.50	0.00	1.00
Recreation*Dist	-0.10	853.00	0.00	1.00
Elevation*Dist	-0.01	0.00	-5.88	0.00
Temp*Dist	-0.01	0.01	-0.88	0.38

Table 2. Continued

	Estimate	*SE*	*z*	*P*
Detection				
Intercept	-4.80	1.57	-3.05	0.00
Sand	-0.26	0.10	-2.66	0.01
Woodland	-0.26	0.14	-1.79	0.07
Shrubland	-0.12	0.16	-0.76	0.45
Manchineel	0.11	0.28	0.39	0.69
Recreation	0.60	0.48	1.26	0.21
Elevation	-0.09	0.11	-0.86	0.39
Water	-0.05	0.46	-0.10	0.92
NDVI	0.26	0.26	1.00	0.32
Temp	3.13	1.67	1.87	0.06

Figure 4. St. Croix ground lizards dispersed in all directions from the 2008 release sites (black squares inset map). Color scale indicates number of lizards per 30 m^2 grid cell (A). The detection of St. Croix ground lizards was independent of dispersal (B).

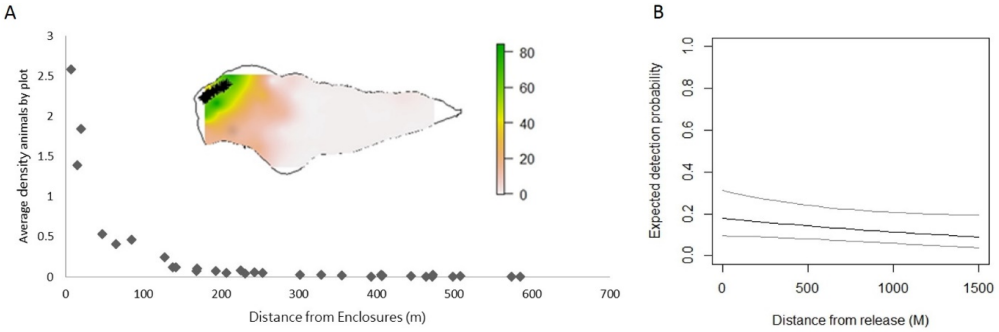
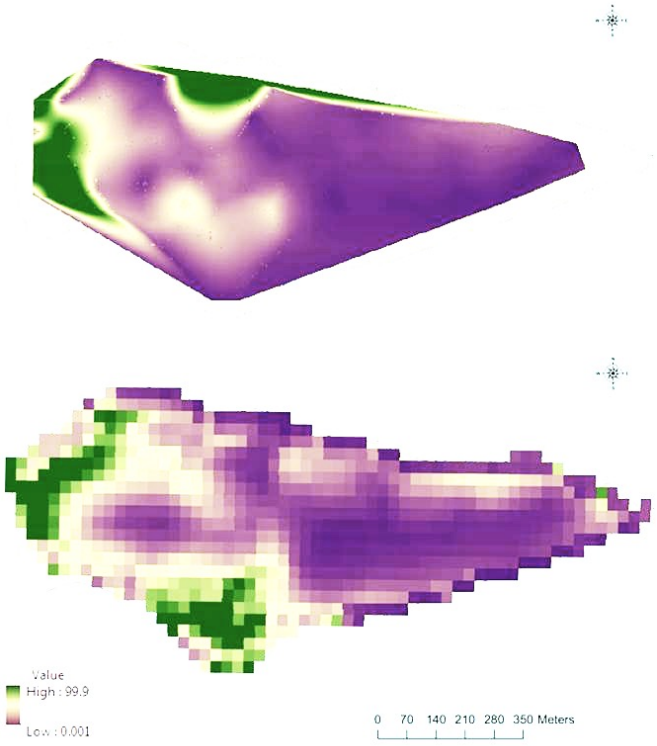


Figure 5. The current (A) and future (B) population state of St. Croix ground lizards on Buck Island. The future abundance was fit with the binomial *N*-mixture model parameters on a 30 m^2 scale. The abundance ranges from 0 (purple) to 100 (green) individuals per grid cell.



significant ($R^2 = 0.912$; $F = 75.86$, df = 30; $P < 0.001$). The model indicated that detection did not vary at increasing distance-from-release. Detection was density-independent, presumably because our survey methodology and length of surveys was sufficient if a lizard was present, even if local density was low (Fig. 4).

Current and Future Population Size

We spatially interpolated the population abundance at sites across the entire island using the final May 2013 model accounting for latent abundance and detection bias (Fig. 5A; AICc: 940.26, $P = 0.46$). The interpolation estimates the population size throughout the island, not only at the survey sites. The island-wide lizard population in 2013 was estimated at 1,473 individuals (95 % CI: 940 - 1,802). The final model predicts lizard occupancy across Buck Island reaching 8,336 individuals in the post-dispersal future population state (95 % CI: 6,590 - 10,501). The model indicated areas across eastern portions of Buck Island where the lizard had not yet been found as suitable for St. Croix ground lizards (Fig. 5B).

Discussion

We estimated the current and future population states of St. Croix ground lizards on Buck Island by incorporating biologically relevant covariates like dispersal and operative temperature in occupancy models and integrating a spatial interpolation model with an *N*-mixture model. Spatially extending the site-specific model results allowed us to estimate abundance across the whole island at the present time-step (2013) and project the model parameters across the island to predict the future population state after lizards had occupied all areas of habitat. We found an effect of elevation and distance-from-

release on abundance, but not observers' ability to detect presence. We believe that dispersal is continuing, and it will have ended when distance-from-release is no longer a significant covariate related to latent abundance. In this case, the island will occupy all areas of Buck Island where suitable habitat exists, and possibly some areas where unsuitable habitat exists. If our predictions are accurate, the future population size will continue to increase up to 6,590 - 10,501 lizards. Simulated data with marked and counted animals using known-fate (capture-recapture) and *N*-mixture models have provided evidence that a sample of marked animals is representative of the population of interest, and conversely that N-mixture models are representative of the abundance of the population (Zipkin et al. 2014, Schmidt et al. 2015). One view is that a combination of intensive (capture-mark-recapture) and extensive (unmarked) datasets will produce the most robust estimates of population states. The limitations and risk related to marking small (<10 g) endangered burrowing lizards precluded extensive marking of any subset of this population for comparison. However, detection probability of marked St. Croix ground lizards during the translocation event (range: 20.1 - 25.1%) was very similar to detection probabilities in this study (Treglia and Fitzgerald 2011). The distribution and abundance predictions from this study are easily testable through application of the same methodological approach with future data collected at the same survey sites. As such, we recommend the abundance of the St. Croix ground lizard monitored at least every five years to maintain consistency in the time interval between the translocation and the first abundance survey post-translocation.

We found that a biologically relevant covariate, operative temperature, improved the fit of the *N*-mixture model because lizards are selecting for sites within their operative temperature. Incorporating operative temperature also improved our ability to model the population size of St. Croix ground lizards on Buck Island, with lower operative temperatures correlating with very low abundance and detection of lizards across all sites. We can presume this is because fewer lizards were available for detection at low operative temperatures. Surprisingly, the operative temperature did not vary significantly among habitat types. Individuals used all vegetation types, but we observed more lizards at woodland (41.0 %) sites and fewer lizards at forest (34.3 %) and shrubland (24.7 %) sites. Woodland sites, where we observed most lizards, were wetter with less leaf litter and less canopy than the other two habitats. Forest and shrubland sites are typically drier, and these sites had, respectively, more canopy (higher NDVI) and dense understory. The habitat associations we used are different than reported in previous studies of the species, where variables such as 'sun patches', 'deep leaf litter' were important to relative abundance (Philibosian and Ruibal 1971, McNair and Lombard 2004). The Buck Island population lives on an island with more topography and higher elevation (0 – 70 m) than the other three populations, which occur on islands l - 10 m above sea level. We found a negative correlation of this species' abundance and elevation. A negative interaction between high elevation and distance-from-release sites indicates that lizards are dispersing around rather than over the peaks on Buck Island. The highest ridges are also areas that are relatively hot and dry. Overall, the uneven distribution of lizards on Buck Island suggests that current

reforestation actions taking place as part of a holistic restoration program will also serve to enhance habitat for the St. Croix ground lizard throughout the island. In particular, planting woodland species should create a matrix of sun and shade that increases opportunities for effective thermoregulation over a greater areal extent.

Our models lead us to predict that St. Croix ground lizards will continue to disperse and eventually occupy areas across the entire island. The model predicted habitat for lizards at the site where we observed two adult male individuals in the eastern part of Buck Island in 2013 (Fig. 3). Besides the two adults we observed in 2013, St. Croix ground lizards have not been observed in the east again, despite 18 formal surveys and during three years of rodent pest control across the island by biologists purposefully looking for St. Croix ground lizards during their work. Outliers are mathematically certain in dispersing populations of reintroduced animals (Yott et al. 2011), and the dispersal distribution of St. Croix ground lizards indicates low densities can exist across the entire island. That we observed two outlying individuals lends confidence to our approach in using distance-from-release in the models. Similarly, studies measuring movement of translocated and resident species have found linear and geometric trends in movements of translocated musk turtles (Attum et al. 2013) and patterns related to least cost pathways for translocated wild ass (Davidson et al. 2013).

Recent conservation challenges such as invasive species, climate change, and the increasing realization that population persistence will require human intervention call for continual development of methodological and modeling approaches. While the challenge of estimating new population states is old, creating reproducible analytical methods that

can account for spatial and biological heterogeneity is more relevant today than ever (Sexton et al. 2009). New models are emerging that allow for the inclusion of biologically relevant parameters and processes in a landscape context. These sorts of approaches, like the one we have taken in this work, should become increasingly useful to understanding the plausibility and limits of conservation introductions and to confronting invasive species problems (Sutherland et al. 2015, Yamaura et al. 2016). Population size of translocated species and invasive species is difficult to model, especially when populations are growing, dispersing, and occupying new habitats. Including mechanistic covariates in models improves the ability to approximate population states over time and make hypotheses for the future of reintroductions and invasions (Seebacher and Franklin 2012, Kearney and Porter 2009). We demonstrated one way to assess the population state of dispersing individuals by integrating models accounting for latent abundance, covariates related to the biology and movement of a focal species, and spatial models. Population state estimation using the workflow presented here can present opportunities to test predictions related to population state estimation and more generally biologically driven hypotheses to enhance the characterization of new populations before individuals have arranged themselves and/or arrived to all available habitats.

CHAPTER III

REPATRIATING SPECIES WHEN THREATS STILL EXIST

Introduction

The majority of island endemics lost to invasive exotic mammals over the past 500 years were reptiles, amphibians, and birds (Sax et al. 2008). Endemic species are lost relatively quickly from small islands, and in many cases relegated to exist only on small offshore refuge islands and in captive colonies (Manne et al. 1999). The presumption that these species are destined to occur in small isolated populations in small refugia still leaves them at risk from natural disasters and may send the signal that the main island where they went extinct are permanently uninhabitable.

Humans shape terrestrial ecosystems by changing the configuration of landscape features and introducing novel flora and fauna. Threats and opportunities also exist based on political factors that accelerate restoration of landscapes (Wintle et al. 2011). In the eastern United States, reductions in agriculture allowed regeneration of forests and grasslands, which are sustaining populations of wildlife ranging from red wolves to salamanders (Connette and Semlitsch 2013, Karlin et al. 2016). The recovery of large carnivores like lynx, wolves, and wolverines in Europe is largely due to advances in management of multi-functional landscapes (Chapron et al. 2014). Successional and multi-use forest patches are allowing previously overharvested animals that lost vast habitat like Puerto Rican parrots and White-crowned pigeons to recover in Puerto Rico and around the Caribbean (Earnhardt et al. 2014, Rivera-Milán et al. 2016).

Failure to recognize that regenerating landscapes change the spectrum of threats for extirpated species may stagnate species recovery to their historic ranges. Novel communities and landscapes are inevitable, and restoration in reconfigured ecosystems will require fresh approaches and new norms (Hobbs et al. 2009). Changes in post-industrial landscapes and emerging landscapes are supporting biodiversity differently than in the past. I suggest that threats to island endemic species, like habitat loss and predation pressure from introduced species, can be overcome in many regenerating landscapes. Drivers of extinction take place in a landscape context, and reconfiguration of those landscapes over time also results in the reconfiguration of those threats. This means there may be opportunities for repatriation into newly emergent areas that contain habitat and natural refugia that were not present during historic extirpation events. This may be true for islands where landscapes have entered a new state, even when perceived historic drivers of extinction like invasive predators still occur.

Already, new ideas are emerging for the reintroduction of species to their historic range (Stier et al. 2016). For example, the clouded leopard was extirpated on Taiwan but is now a candidate for repatriation as the prey base has returned to regenerating forests (Chiang et al. 2015). The reintroduction of a native predator to a relatively large island like Taiwan (35,801 km^2) is a different ecological case than the reintroduction of native prey species when invasive predators are still present. For example, West Indian islands are on average 345 km^2 with historic losses of 30 – 97% forest cover and conservation concerns at a competing scales and complexities. One of the most endangered lizards on Earth, the St. Croix ground lizard (*Pholidoscelis polops*), lost 99.97% of its historic

range on mainland St. Croix (217 km^2) after the introduction of a predator, the small Indian mongoose (*Herpestes auropunctatus*), which coincided with conversion of 90% of the island's forests to agricultural pasture. St. Croix ground lizards persisted on two very small offshore cays where there were no mongooses (Henderson 1992). Translocations were successful to two additional small islands without mongooses (Fitzgerald et al. 2015). Repatriation to the mainland of St. Croix has not been a recommended recovery action due to the persistent threat of mongoose predation on St. Croix forfending any repatriation to St. Croix (Meier et al. 1990). Our aim in this paper is to explore the alternate view, that even though mongooses are still present on St. Croix, reconfigured landscapes create new opportunities for repatriation of the St. Croix ground lizard.

Where novel landscapes exist, so may novel opportunities for species-specific conservation actions. We developed a prioritization scheme (Dawson et al. 2015) to determine the landscape areas appropriate for repatriation based on changes in the historic (1750) and current (2016) configuration of land cover. We assessed present-day lizard habitat using models developed with data from the largest extant population on the largest offshore island. We also assessed the future capacity for mongoose control in potential translocation sites. Our work demonstrates how changing landscapes present new opportunities for restoration in historic ranges and on islands, even when threats exist on a broader landscape scale.

Methods

Landscape level change on St. Croix, 1750 – 2016 and impact of mongoose

St. Croix is a single land bank (21,470 ha), erupting from the ocean where tectonic plates merged, surrounded by trenches greater than 1,000 m (Case and Holcombe 1980). The west end of the island receives 125 cm of rain annually while the east end receives 75 cm of rain (Bowden 1968). Four offshore islands total 84 ha additionally.

The landscape of St. Croix has been mapped extensively since 1750, but only one surviving map of land cover from 1750 exists today (Hopkins 1989). The acreage of plantations increased in all areas from 1742 to 1754 (Westergaard 1938) transitioning from cotton to sugarcane during 1754 to 1800 (Tyson 1992). Rats fed on the sugarcane, precipitating the 1872 introduction of mongooses to control rats (*Rattus rattus* and *Rattus norvegicus*). By 1917, nearly 90% of the native forests and woodlands that covered 90% of St. Croix were cleared for agriculture or logged for timber (Ward et al. 2000). Sugar cane cultivation virtually ceased by the late 1950s (Atkinson and Marín-Spiotta 2015). Since then, secondary subtropical forests returned to St. Croix, and in the entire West Indies, with naturalized tree species and novel assemblages colonizing formerly agricultural lands (Atkinson and Marín-Spiotta 2015).

The earliest records of the impact of the loss of the St. Croix ground lizard begin in the 1930s. It was extirpated from the east end of St. Croix by 1920 and the last individuals were seen in Frederiksted on the west end of St. Croix by 1969 (Dodd 1978). Fortunately, two populations of St. Croix ground lizards persisted on Protestant Cay (2.6

ha) and Green Cay (4.3 ha) because mongooses were never established there (Dodd 1980, Thomas and Joglar 1996). Anecdotal reports attributed increases of sugarcane grubs in the fields and centipedes in the town of Christiansted to the disappearance of lizards (Nellis and Everard 1983). Mongooses are still common, and St. Croix harbors one of most densely packed populations of mongooses across all Caribbean islands. However, mongoose presence and density is not uniform across the island (Horst et al. 2001).

Two recent conservation introductions indicate St. Croix ground lizards are relatively easy to establish in new areas. A population was established on Ruth Island (9.7 ha), a dredge-spoil island, with only nine propagules from Protestant Cay in 1989, and a translocation from Green Cay to Buck Island (69 ha) with 57 individuals in 2008 was successful (Fitzgerald et al. 2015). Between 1500 - 3000 individuals occur on these four small islands (total 84.9 ha) today, all of which are vulnerable to unplanned events like hurricanes, predator invasion, and habitat degradation from plant invasion.

Landscape data layers

We collected data related to protected areas, the level of mongoose threat, landscape cover, and habitat associations of the lizards. The 1750 historic map of St. Croix was used to determine the historic land cover (Hopkins 1989). We delineated land cover types on St. Croix in 1750 by overlaying the borders of the island and its waterways onto a current map using the 'DigitizingTools' plugin for QGIS. We then used the QGIS 'Geoprocessing Tools' to quantify land cover in 1750 into urban, woodland, forest, edge forest, shrubland, water, pasture, grassland, salt ponds (Fig. 6).

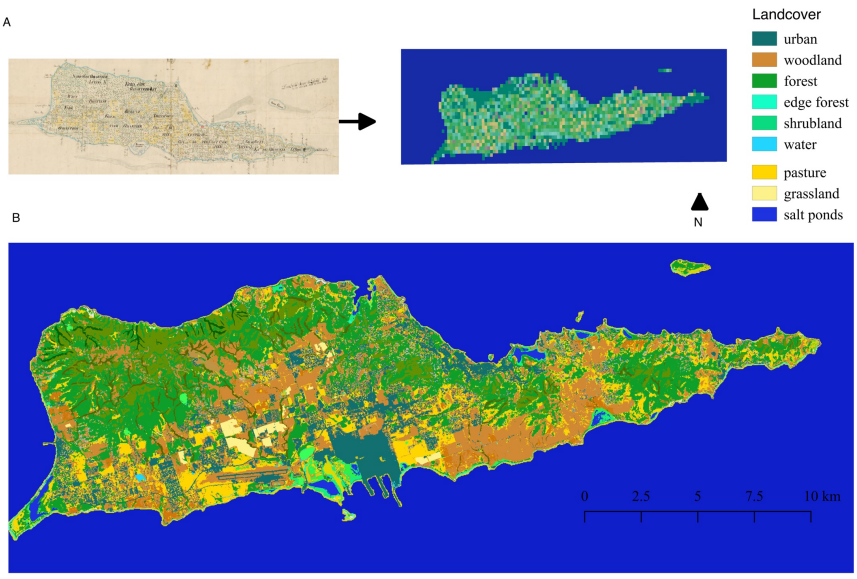
Modern land cover was classified into 76 types by Gould et al. (2007). We collapsed these into the same categories on the 1750 map. We lumped the percent of woodland and shrubland into one category and edge forest and forest into a second category. We also compared urban land cover and pastures including agriculture. We did not compare the land cover contributions from water or salt ponds because these do not directly affect the areas that ground lizards utilize. We compared the amount of land cover (ha) in each class using paired Welch's t-tests.

Lizard habitat and population estimation

The St. Croix ground lizard is a small actively foraging diurnal ectotherm that uses a variety of cover types as habitat. We created a lizard habitat layer using the results of the model of the occupancy and population size of St. Croix ground lizards on Buck Island in 2013 (Angeli et al. 2017). To assess the population on Buck Island, we used *N*-mixture modeling to account for latent abundance and low detection of the species (Fitzgerald et al. 2015). We conducted visual counts of unmarked animals with multiple observers at 42 sites throughout Buck Island. The model was fit in program R package 'unmarked' with a negative binomial *N*-mixture occupancy model (version 0.10.2, Fiske and Chandler 2011). We found that by 2015, St. Croix ground lizards had dispersed from the translocation site to occupy 68.9% - 89.1% of Buck Island. Detailed results are reported in Table 2 and Fitzgerald et al. (2015).

Using the best fit *N* –mixture model results from Buck Island (P=0.64), we had prior knowledge that habitat type (*Woodland, Shrubland, Manchineel Forest, Forest),* elevation (*Elevation*), substrate (*Sand, Water)*, canopy cover (*NDVI =normalized*

Figure 6. The 1750 and 2016 landcover in St. Croix, U.S. Virgin Islands. The digitized map (A) was based on the handdrawn map by J. Cronenberg and J. von Jaegersber (Hopkins 1989). The landcover communities in 2008 (B) reproduced with permission from US. Puerto Rican Gap Analysis were matched to the digitized historic landcover types (A).



difference vegetation index), and land surface temperature (*Temp*) were important to the lizard's distribution (Table 2). To avoid using the distance to dispersal (*Dist*) required for estimating the dispersing population on Buck Island, we set a new data frame value for *Dist = 0.* The remainder of the dataset was as described in in Angeli (2017) and Fitzgerald et al. (2015). The digital elevation model (DEM) for St. Croix was based on the U.S. Virgin Islands topography model (Gesch 2007). Because the DEM has a 1 arc-second or 30 m^2 grid cell, all subsequent references to lizard habitat use a 30 m^2 scale. We used the 'predict' function for the rasterized data from the top model to fit the model parameters to the St. Croix dataset. We assigned each 30 m^2 grid cell a score for lizard habitat from 1 – 25, where 1 – 6 were not suitable, 7 – 12 were maybe suitable, 13 – 20 were suitable, and 21-25 were most suitable (Fig. 7). To estimate abundance in each area, the model produced a population estimate for each grid cell of each suitability category. These estimates were summed to obtain an estimate of lizard habitat *A* for the entire area (Table 2).

Predicting suitable sites for repatriation

Protected areas consisting of both public and privately held land were considered for repatriation. The repatriation areas were ranked using a formula,

$$Repatriation\ score = \sum_{1}^{s} T_i * A_i * M_i \text{ (eq. 1)}$$

where the threat *T* and/or ability to manage mongoose (1 or 0.5) at each site *s* was multiplied by the total lizard habitat *A* and mitigation efforts required or on-going for management of mongoose *M*. The habitat model for small Indian mongoose on St. Croix

was produced by Gould et al. (2007). They used habitat variables from an in-depth study of mongoose on St. Croix in Hoagland et al. (1989). All suitable areas for mongoose were represented as a binary presence (1) or absence (0) value. Their results showed that mongooses were not evenly distributed across St. Croix and their population density was variable. Mongooses were absent from 795.92 ha (3.65%) of St. Croix, most notably in southern areas of the island where there is much suitable habitat for St. Croix ground lizards (Fig. 7). The percent of the protected area with mongoose habitat was multiplied by mongoose control capability *T*. Capacity to control mongoose *M* was assessed based on the ability of staff to engage in trapping or the feasibility of constructing a mongoose-proof barrier based on length (Xcluder-type, from Young et al. 2013).

Results

Landscape change in St. Croix

In 1750, less than 11% of land was devoted to pasture or agriculture and 42% of land was forest cover. Less than 5% of the land was urban. The remaining 42% was undifferentiated in the historic map among woodland, shrubland, and edge forest. The current map showed St. Croix with 31% forest cover. Succession of uncultivated fields to shrubland, woodland, and edge forest brought the total to 25% of St. Croix on the current map. Pasture (including agriculture) comprised 32% of land today. Less than 12% of St. Croix was urban in the current map. The percent of habitat shows no significant differences between the historic and current land cover categories were found, indicating trends towards reconfiguration of the landscape on St. Croix that

includes similar amounts of forest and grasslands as were present 250 years ago (t=0.01, df=4.26, *P*=0.98).

Lizard habitat on St. Croix

The habitat models estimated that St. Croix can support 142,421 lizards across 1,169 hectares of suitable habitat. We identified 19 protected areas that each contained 2.4% to 100% habitat (Table 3). The population models indicate a total 21,469 St. Croix ground lizards could be supported in protected areas on St. Croix, based on an average of 8.2 (SD = 4.1, range = 0.0 – 24.0) ground lizards per each 30 m^2 grid cell. The top nine of the 30 protected areas with lizard habitat already have some degree of mongoose control measures in place, or the ability to construct mongoose barriers with less than 3 km of fencing. The areas are displayed cartographically in Fig. 7. Based on the model results and ranking of potential sites, we identified three repatriation sites that have lizard habitat and capacity for mongoose control (Fig. 8).

1. Sandy Point National Wildlife Refuge: The 155 ha Sandy Point National Wildlife Refuge (SPNWR) is located on the southwest end of St. Croix. The mongoose population has been studied and monitored in the refuge and has been reduced through trapping. A mongoose exclusion fence proposed to benefit nesting sea turtles would serve the dual purpose of creating an area with 43.3 ha of habitat for the St. Croix ground lizard. The total length of an exclusion barrier is 2.9 km.

2. Altoona Lagoon: Altoona Lagoon is a 6.8 ha area managed by the USVI Department of Natural Resources and Planning. Our model showed the entire area consists of habitat for the St. Croix ground lizard. Though small, the site is protected and

is equal in size to Protestant Cay and Green Cay combined, where the lizards persisted after extirpation from St. Croix. A wetland adjacent to coastal forests and beach are an important migratory bird area. The total linear length requires an exclusion barrier of 490 m.

3. Southgate Coastal Reserve: The 41.9 ha Southgate Coastal Reserve is managed by the St. Croix Environmental Association. Prior to lizard repatriation, a large feral cat population must be reduced in addition to mongooses. Two feral cat feeding stations maintained by local citizens are located within the reserve (J. Valiulis, SEA, pers. comm), so removal of the cats would require public outreach and education about the effects of small carnivores on lizards. The total areas of Southgate Coastal Reserve suitable for lizards is 19.3 ha. The total linear length of an exclusion barrier would be 1.75 km.

Figure 7. The St. Croix ground lizard could occupy up to 5% of the island of St. Croix, Virgin Islands. The categories are equivalent to rankings of suitability based on threats, habitat associations, and on-going conservation engagement by local actors. The habitat categories are equivalent to ranking of suitability ranking from 1 – 25 where 1 – 6 are not suitable, 7 – 12 are maybe suitable, 13 – 20 are suitable, and 21-25 are most suitable.

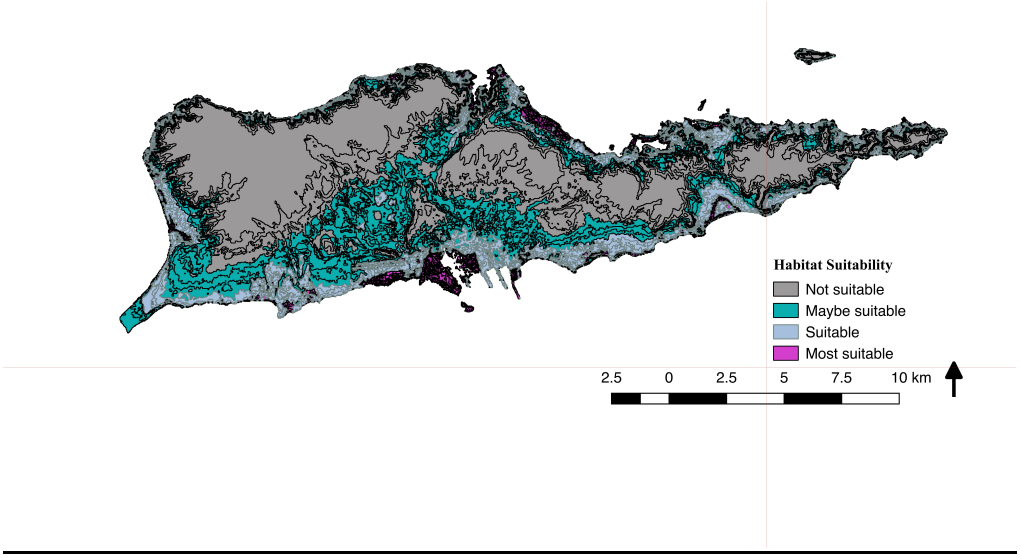


Figure 8. The St. Croix ground lizard lives in four extant populations (top row) on (A) Green Cay; (B) Buck Island; (C) Protestant Cay; (D) Ruth Island. We propose three repatriation sites on St. Croix, U.S. Virgin Islands at (E) Sandy Point; (F) Altoona Lagoon; (G) Southgate Coastal Preserve (bottom row). An *N*-mixture model parameterized for land cover, elevation, soil substrate, land surface temperature, and canopy cover (Angeli et al., 2017) created the predictions based on survey work on Buck Island. The model results reduced to four categories from 'Not suitable' to 'Most suitable'. The inset map indicates where each site is located.

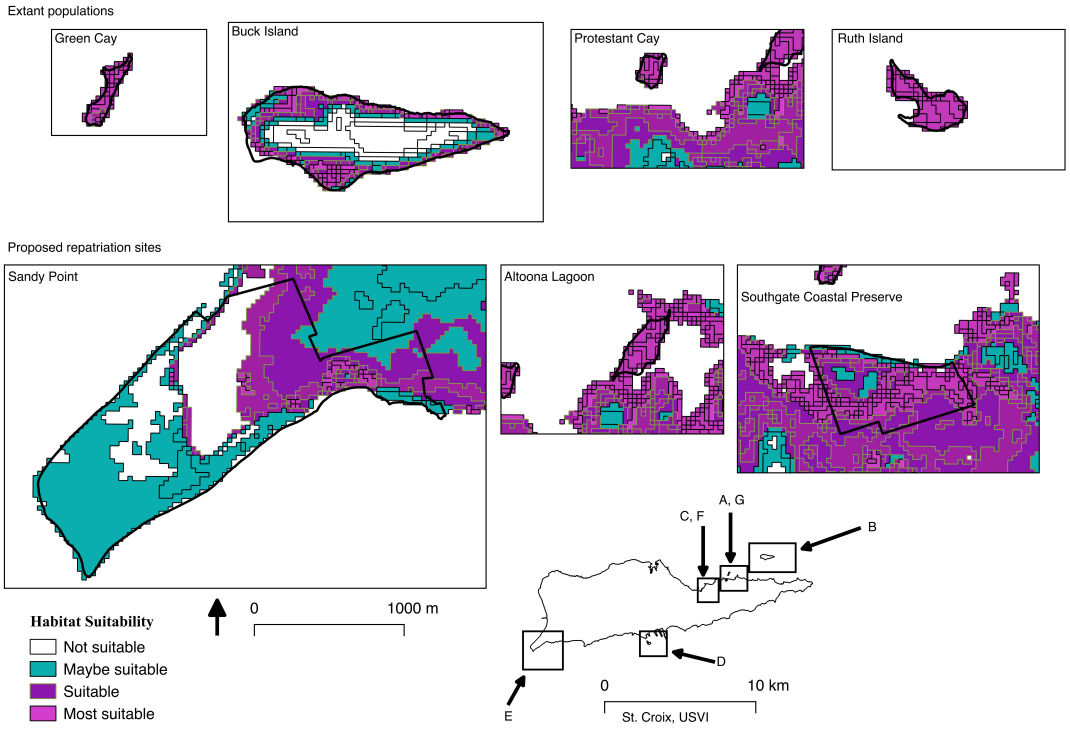


Table 3. A ranked list of the proposed areas identified for potential repatriation of the St. Croix ground lizard, calculated from the combined scores of habitat suitability, mongoose presence, and mongoose exclusion capacity (see text for details). Percent habitat refers to the percentage of the total habitat in the 'suitable' categories: maybe suitable; suitable; most suitable. Abundance was estimated from the model, and summed to obtain an estimate for the entire area.

Protected Area	Area (ha)	Habitat (ha)	% Habitat	Abundance	Rank
Existing populations					
Ruth Cay Wildlife Sanctuary *	9.7	9.7	100.0	461	-
Protestant Cay Wildlife Sanctuary*	2.6	2.5	95.4	151	-
Green Cay National Wildlife Refuge *	4.3	3.0	70.2	499	-
Buck Island Reef National Monument *	69.0	62.0	90.0	2,150	-
St. Croix	**21,755**	**1,169**	**5%**	**142,421**	**-**

Table 3. Continued

Protected Area	Area (ha)	Habitat (ha)	% Habitat	Abundance	Rank
Ranked repatriation sites					
Sandy Point National Wildlife Refuge	155.5	43.4	28.2	1,273	1
Altoona Lagoon Beach Recreation Area	6.8	6.8	100.0	488	2
Southgate Coastal Preserve	41.9	19.3	46.1	1,722	3
East End Marine Park	55.1	14.6	26.6	1,941	4
Salt River Bay National Historic Park and Ecological Preserve	162.3	66.3	40.9	8,193	5

Table 3. Continued

Protected Area	Area (ha)	Habitat (ha)	% Habitat	Abundance	Rank
East Bay and Point Udall	53.5	3.1	5.8	1,829	6
Estate Little Princess	19.4	15.8	81.5	847	7
UVI Wetlands	35.0	6.8	19.4	1,130	8
Derick O. Steinmann Memorial Beach	0.8	0.1	16.1	52	9
Manning Bay Wetlands	29.9	29.2	97.6	1,835	10
Long Point Bay	7.8	2.2	27.9	258	11
Estate Great Pond	12.9	2.1	16.4	478	12
Jack and Isaacs Bays Preserve	120.8	2.8	2.4	1,423	13
TOTAL	701.7	212.5		21,469	-

Discussion

The conservation benefit of repatriation would indicate success of the idea that species can persist in re-emergent landscapes. For this and other similar species restricted to offshore islands, the future is uncertain. While experience indicates that St. Croix ground lizards can be established in areas where mongooses are actively controlled, we also predict that the reconfigured landscape on St. Croix creates refugia for the species that would allow dispersal from founder populations in the protected areas to other habitat. The founder populations where mongooses would be controlled serve as source populations for dispersal into a broader landscape. The expected result is establishment of an island-wide meta-population with sources and sinks.

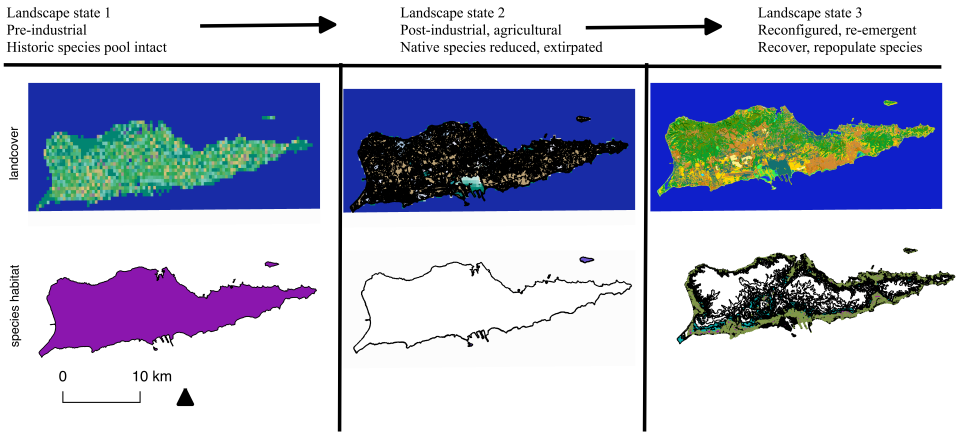
Threat abatement remains a key factor in setting the stage for repatriation of species, especially on islands. However, total eradication of invasive predators on relatively large human-inhabited islands may not be feasible. Landscape-scale modeling, in combination with prior knowledge of natural history and population biology of target species allow for strong predictions on the feasibility of repatriation when threats persist at broad scales. When refuge populations are relatively secure, the risks in repatriation are small in comparison with the potential reward for conservation. Understanding the landscape of threats and using that knowledge to adjust conservation actions can present positive opportunities for restoration of species and rewilding of areas (Figure 9).

Specifically, the uneven pattern of occurrence of mongoose in the past presumably allowed St. Croix ground lizards to persist in isolated areas during a 95-year decline. St. Croix ground lizards can escape mongoose predation by taking refuge in a

variety of anthropogenic structures that are inaccessible to mongooses such as rock piles and behind fencing. It may have been the lack of these landscape features during the period of extensive agriculture that contributed to the demise of the species. Indeed, its last stronghold in the 1960s was along the beaches and vegetation surrounding the Frederiksted Fort (Dodd 1978). The present pattern of occupancy of mongooses creates opportunities for St. Croix ground lizards to inhabit localized areas. The model of Gould et al. (2007) for mongoose occurrence on St. Croix, using field data on mongoose populations (Hoagland et al. 1989), showed numerous areas where mongoose were predicted to be absent that overlap with the priority areas for repatriation of St. Croix ground lizards (Fig. 2). While the models we developed demonstrate the potential for repatriation, they are relatively coarse-grained and cannot quantify smaller patches of refugia the St. Croix ground lizard may occupy. Future quantification of fine-scale configuration of habitat and refugia, combined with studies of habitat selection and mongoose avoidance would serve to test our predictions and provide important information for adaptive management of repatriated St. Croix ground lizards.

Population connectivity can be achieved post-translocation via dispersal (Carroll et al. 2015) and promote demographic and geographic recovery of the St. Croix ground lizard. Two successful translocations of the St. Croix ground lizard on Ruth Island and Buck Island indicate it disperses rapidly throughout available habitats (Fitzgerald et al. 2015, Wolf et al. 1998). The results of survey work conducted from 2013 – 2015 on Buck Island indicate that dispersal of lizard occurs in linear movements from the point

Figure 9. Conceptual framework for repatriation where threats still exist. The landscape state 1 indicates a time prior to selected stressors, here agricultural, industrial, and residential development in St. Croix, USVI. Landscape state 2 corresponds to the inception of technological advances prior to lessening agricultural land burdens in 1950 – 2000. Landscape state 3 is the current state of the land which corresponds more closely to landscape state 1 than 2, and species habitat returns as changing landscape configurations alter landscape level threats.



of that introduction. It is reasonable to believe that when individuals are released, they will radiate linearly outward shortly after introduction and become dispersed later. To promote opportunities for dispersal from secure propagule repatriation areas into surrounding habitat, a barrier that is lizard-permeable would facilitate natural dispersal. Mongoose exclusion fences are used to protect vulnerable populations of wildlife in numerous locations. For example at Ka ʻena Point, Hawaiʻi, exclusion fencing protects young Laysan albatross from many predators, and their population is increasing (Young et al. 2013). Multiple areas on St. Croix are proposed for repatriation of the species. Just the top three of nine possible repatriation sites, the species' range increases by 180%. The short-term risk to the species is low, because the new population on Buck Island is greater than 2,000 individuals, and the lizards are doing well on the other offshore cays (Fitzgerald et al. 2015). Monitoring would reveal the degree of successful dispersal into adjacent areas.

This case also serves as a model for reinvigorating stagnant recovery for species similarly restricted to refugia on islands and mainlands. Repatriation where threats still exist is dependent on the landscape of threats but also the suitability of the species for repatriation and rewilding. For example, the Milu (*Elaphurus davidianus*) became extinct from the combination of hunting and land reclamation in China at the turn of the 20th century, but a wild population became established in 1998 from animals that escaped from a nature reserve. Now, more than 300 Milu descendent from the escaped animals occur in the wild (Yang et al. 2016). In New Zealand networks of refugia are already envisaged where tuatara, kiwi, and other species can become repatriated to their

former range (Ostendorf et al. 2016). Spatial variance in threats in restored and regenerating landscapes will allow native species to return to native habitats.

Repatriation experiments such as we have proposed can be tested through careful implementation and monitoring and provide important data for moving forward. Risks of not learning how to repatriate species are great over the long term. Small populations will remain vulnerable to sea level rise and anthropogenic disasters, and biodiversity will increasingly be perceived as only able to hang on in refuge populations. Conservation translocations used in combination with localized threat abatement and taking broader landscapes into account hold much promise for species conservation.

CHAPTER IV

HOTTER TEMPERATURE TOLERANCE FOR ECTOTHERMS FACING THREATS FROM INVASIVE PREDATORS

Introduction

Novel species interactions, especially between introduced predators and prey, can be a powerful driver of biological change (Alexander et al. 2015, Courchamp et al. 2003). For example, morphology of native snakes changed to adapt to invasive cane toad predation in Australia (Phillips and Shine 2004) and genetic diversity of anoles declined on islands with invasive rats in the Bahamas (Gasc et al. 2010). The susceptibility of small ectotherms to predation from exotic species may depend, in part, on the strength of trade-offs related to thermoregulatory behaviors or the influence of predation risk may cause lizards to shift to new microhabitat (Huey et al. 2003). For example, if ectotherms have evolved to select high body temperatures, the need to evade introduced novel predators may interfere with thermoregulatory behaviors like shuttling (Seebacher 2005, Sears and Angilletta 2015). Lizards may be forced either to be active at later, warmer times of the day and in warmer microclimates or to reduce their activity in open, warmer environments and use cooler microclimates not frequented by a predator. A shift in use of new microhabitats to reduce predation risk could potentially cause thermal tolerances to change quickly under new conditions. While the effect of invasive predators on native prey has been studied across behavioral, demographic, morphological, and ecosystem scales (Phillips and Shine 2004, Didham et al. 2007, Hoare 2007), physiological responses to novel predators are much less documented and merit more study.

Emerging evidence exists to indicate that physiological traits change over generations in response to abiotic conditions some of which I summarize in this paragraph by trait. First, the critical thermal minimum (CT_{min}) changes with broad environmental conditions but also within populations of species (Tuff et al. 2016, Muñoz et al. 2014, Leal and Gunderson 2012: Overgaard et al. 2011, Cruz et al. 2005). The evolution of cold tolerance (CT_{min}) enhances individual survival of lizards in two ways. First, nocturnal thermal environments are relatively homogeneous (Kearney and Prevadec 2000) so adapting to colder conditions negates the need to behaviorally thermoregulate. Second, selection favors the ability to tolerate increasingly colder night temperatures (Muñoz et al. 2014). By contrast, there are reasons to expect CT_{max} would be more directed. Diurnal landscapes are thermally complex, and individuals can respond to heat by selecting cooler or hotter microhabitats to stay under heat tolerance thresholds (Huey et al. 2003). Patterns of heat tolerance are consistent across latitudes and seasons within species, a pattern hypothesized to occur because animal's themoregulatory behavior across thermally-complex, diurnal landscapes buffers adaptive changes in CT_{max} (Overgaard et al. 2011, Angilletta et al. 2007). And indeed, less evidence indicates that the critical thermal maximum (CT_{max}) can shift in response to environmental or biotic conditions among populations of a single species and shifts could be attributable to founder population characteristics and adaptive capacity of founding populations may contribute to phenotypic expression (Leal and Gunderson 2012, Kolbe et al. 2012).

While considerable attention has been given to testing the effects of abiotic factors on thermoregulatory traits, the effects of novel predators on thermoregulatory traits of native prey are largely undocumented. New patterns of predation could drive shifts in thermal tolerance, and may be a potentially important mechanism by which ectothermic prey may adapt to changing predation pressures. The exploitation of new patches and activity times are two ways that the introduction of a novel predator could shift thermal tolerances. In the case of the tropical low-land species, cooler temperatures are not available during diurnal activity periods, and upper shifts beyond the range of endothermic temperature tolerance may be the more important driver. If this hypothesis is true, then we predict that thermoregulatory behaviors disrupted by predators in diurnal landscapes would overwhelm behavioral buffers on CT_{max}, and natural selection would lead to increasing CT_{max}. There is some evidence in support of upward shifts in CT_{max}. Upper thermal limits in *Petrolisthes* crabs and *Drosophila* flies occurred in experimentally established populations (Buckley and Huey 2016). In the wild, ants from urban heat islands survived longer at hotter temperatures than ants from cooler rural communities without corresponding adaptations to cold exposure (Angilletta et al. 2007). Similarly, the translocation of adult *Anolis* lizards to heat islands showed that surviving individuals were also the individuals with the greatest performance breadth (Logan et al. 2014). Fewer patterns across upper than lower tolerance traits of wild individuals and upper limits on thermal tolerance due to combinations of environmental and biological conditions indicate some constraint on adaptation and acclimation (Hoffman et al. 2013). Alternatively, because the effects of predators and other stressors

on individuals are shared within large populations and some changes are unpredictable, some obscuration of population-level changes to novel conditions may exist in wild populations (Kingsolver and Pfennig 2007).

Because upper and lower thermal tolerance in wild squamates appears to respond to some abiotic stressors, we predict that individuals may be able to cope with biological stressors, like novel predation pressure, by acclimation or adaptation of thermal tolerance (Diamond 2016, Blows and Hoffmann 2005). Two indices devised to track the impacts of changing environments on physiology showed strong patterns globally. Warming tolerance (*WT)*, or the difference between CT_{max} and mean annual surface temperature of the habitat (T_{hab}), is positively correlated with latitude (Deutsch et al. 2008). Similarly, the thermal safety margin (*TSM*), the difference between an organism's optimal temperature for performance (T_{opt}) and T_{hab}, changes positively with latitude (Deutsch et al. 2008). Selection for increasing CT_{max} or reducing T_{pref} exists when a narrow margin between the selected body temperature (T_{pref}) and CT_{max} reduces survival, for example if overheating occurs rapidly during predation events. Therefore we propose looking at an "overheating safety margin" (*OSM*), the difference between CT_{max} and T_{pref} (mean preferred body temperatures in a thermal gradient) as a measure of the intrinsic tolerance of lizards to overheating. We expect to find evidence of selection on *OSM* on one of either components, CT_{max} or T_{pref}. Any increases in *OSM* would decrease an individual's risk of overheating under stress, such as during a predation attempt.

Our aim was to gain insight into how species' physiological traits respond to novel predator – prey interactions. We studied the physiological traits of Puerto Rican

ground lizards (Teiidae: *Ameiva exsul*) coexisting with a novel predator, the Small Indian Mongoose (*Herpestes auropunctatus)* with populations in habitats without the predator. As in other species in the family Teiidae, Puerto Rican ground lizards thermoregulate close to their upper thermal limits (Gifford et al. 2012, Martin and Huey 2008). As a consequence, the average *OSM* for teiids to-date is less than for any other squamate group (Martin and Huey 2008). Both mongoose and Puerto Rican ground lizards are diurnal, active foragers with similar active body temperatures of ~ 37 - 39 °C and critical maximum temperatures ~ 45 °C in the wild (Gifford et al. 2012, Nellis and McManus 1974). If trade-offs exist between thermoregulatory and predator-evasion behaviors, natural selection would favor individuals with greater *OSM* where mongoose occur if thermally favorable microhabitats are not available because of predation risk. By contrast, we should find smaller *OSM* in populations naïve to mongoose. We predicted that the direct action of removal of Puerto Rican ground lizards with low CT_{max} by predation from mongoose either due to an inability to explore warmer microhabitats or time periods would drive a shift to higher $CT_{max.}$ A lower T_{pref} in mongoose-exposed populations lizards would not maximize metabolic and predator-evasion behaviors such as sprinting and endurance. If these predictions are supported, then Puerto Rican ground lizards and mongoose co-exist today partly due to adaptive physiological mechanisms.

Methods

To investigate selection on heat tolerance due to predation, we studied the Puerto Rican ground lizard (*Ameiva exsul*), a forest-edge heliothermic ectotherm. In the Puerto Rican Bank, Puerto Rican ground lizards are found on 85 cays and islands, encompassing

936,702 ha across coastal habitats less than 500 feet high (Powell and Henderson 2012, Rivero 1998). This sexually dimorphic species reaches 200 mm snout-vent length and has a lifespan of five to eight years (Angeli and Weidler unpublished).

We considered body size (snout-vent length) as a proxy of fitness (Endler 1986). Rodriguez-Ramirez and Lewis (1991) found that Puerto Rican ground lizard size is linked to the quality and quantity of resources consumed. Larger males sire a greater proportion of eggs in greater numbers of clutches than smaller males (Lewis et al. 2000), and larger females have greater numbers of eggs per clutch (Rodriguez-Ramirez and Lewis 1991). For individuals bred in large pens in-situ in western Puerto Rico, SVL correlated to male mating success and female fecundity (Lewis, Tirado, and Sepulveda 2000). Here we assume the same conditions for individuals in the wild, so we use body size as our established fitness proxy (Jakob et al. 1996).

Sampling sites

We selected sampling sites based on two factors: (1) the sites' environmental gradients to encompass the range of environmental conditions that lizards experience, and (2) the exposure of Puerto Rican ground lizards to mongoose. First, precipitation and temperature influence the traits CT_{max} and T_{pref}. (Clusella-Trullas et al. 2011). To create paired environmental conditions across sites with and without mongoose, we used data from 1980 to 2010 on annual rainfall ($T_{env\text{-}pre}$), average temperature of the median month ($T_{env\text{-}avg}$), minimum temperature of the coolest months ($T_{env\text{-}min}$), and maximum temperature of the hottest months ($T_{env\text{-}max}$) from 28 long-term weather stations in Puerto Rico (Regional Climate Center, accessed Oct 2015). Shapiro tests showed the climate

data were normally distributed. We used an NMDS to reduce the dimensionality of the environmental data presuming co-dependence of some but not all of the variables to select a preliminary set of field sites across the species range (McCune and Grace 2008). The first axis primarily described a gradient of low to high precipitation. The second axis primarily described a gradient of cool to warm sites. All sites are surrounded by a matrix of shrublands, woodlands, developments, and forests (Appendix C).

Of the 28 sites, 19 had mongoose present. We used six criteria to gauge the exposure of Puerto Rican ground lizard populations to introduced mongoose (Appendix C). These criteria were: historical occurrence records, habitat suitability based on a GAP Analysis, incidence of rabies, fragmentation of habitat, whether the area was a plantation/agricultural, and visual confirmation (Appendix C). Mongoose were considered absent from a site when none of the criteria were met.

We selected fives sites from locations exposed to mongoose and five in areas without evidence of mongoose. A Wilcoxon rank sum test found no differences in the NMDS scores between the sites with mongoose present and sites without mongoose on the first (W=16, P=0.53) or second axis (W=11, P=0.83) indicating overall representation of environmental conditions across the groups.

Sample size

We used a power analysis to determine the number of animals to sample across the five mongoose-exposed and five naïve populations during the temperature trials of the research (Cohen, 1992). We used the formula for the effect size (d) in a balanced one-way analysis of variance power calculation,

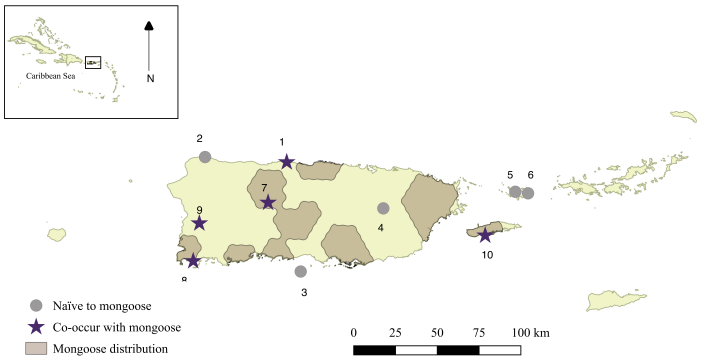
$$d = \sqrt{\frac{\sum_{i=1}^{k} p_i\,(u_i - u)^2}{\partial^2}}, \text{ (eq. 1)}$$

where p_i is n_i/N, n_i is sample size per group, N is the total number of observations, u_i is the mean of the group, u is the mean of all observations, ∂ is the pooled standard deviation of the groups (Cohen 1988). The test allows distinguishing a 1°C difference among populations. We determined that at each of our 10 populations, sampling 5 – 10 individuals would avoid 95% of Type 1 and 80% of Type II errors. With the range of sample sizes in our study, the effect size ranges from 0.4 – 0.6 (Wilcox 2011).

Measurement of physiological traits

We captured 71 individuals from ten populations by noosing (Fig. 10). We measured preferred body temperature (T_{pref}), critical thermal minimum (CT_{min}) and critical thermal minimum (CT_{max}) of each individual (Hertz et al. 1993). The T_{pref} of each individual was measured by allowing the animal to thermoregulate in a temperature gradient of 20 to 65 ºC. The thermal gradient was constructed from plywood measuring 4 feet long by ½ foot wide and 3 feet tall. All animals were in the gradient for at least one hour and when we assumed the animal achieved its T_{pref} when we measured four or more temperature readings taken 5 min apart with a K-type thermocouple in the cloaca had not deviated more than 1 ºC (Hertz et al. 1993).

Figure 10. A map of sites where Puerto Rican ground lizards (*Ameiva exsul*) were sampled to measure physiological traits. Stars denote sites where mongoose occur; circles denote areas without mongoose. Shaded areas are the current distribution of mongoose in Puerto Rico. The populations are numbered as follows: 1: Arecibo, 2: Borinquen, 3: Caja Muertos, 4: Cidra, 5: Culebra, 6: Culebrita, 7: Dos Bocas, 8: Lajas, 9: Mayagüez, 10: Vieques. See text for details on Arecibo (1) and Mayagüez (9), which while outside of mongoose habitat suitability, fulfill alternate criteria for mongoose occurrence.



We measured CT_{max} and CT_{min} of individuals within one hour of achieving their preferred body temperature. This was done so that the magnitude of the temperature change during temperature tolerance trials did not confound the temperature at which an individual achieved its thermal limits (Angilletta 2009). We measured the body temperature of lizards with a K-type thermocouple inserted in the cloaca of the animal at the moment it displayed its maximum or minimum temperature tolerance. We measured heat tolerance by enclosing individuals in a confined space with an incandescent heating lamp until the onset of seizures (Winne and Keck 2005, Lutterschmidt and Hutchison 1997). We measured cold tolerance of animals in a quart ziploc$^{(R)}$ container that was floated in a 5 gallon ice bath of 5°C. We flipped animals from their ventral to their dorsal side every 30 seconds to check for loss of a righting response. All measurements were taken between the hours of 10AM and 2PM, corresponding with these lizards' peak activity period (Lewis and Salvia 1987). After physiological testing, a resting period allowed animals to recover before release at the site of capture.

We calculated *OSM*, the difference between T_{pref} and CT_{max}, for each population. We also calculated the warming tolerance (*WT*) and thermal safety margins (*TSM*) for each population to determine effects of the environment on these traits. We show data from six additional sites with and without mongoose on the mainland of Puerto Rico where operative temperature of *Ameiva exsul* was taken at each across six microclimatic conditions – Full shade – bare ground, leaf litter; Partial sun – bare ground, leaf litter; Full sun – bare ground, leaf litter (Appendix C). We used the environmental data from the long-term climate centers to create determinations of site characteristics.

Analyses

We used nonparametric Wilcoxon rank-sum tests to determine differences in thermal traits between individuals and populations. Variance in all three variables was homogenous within individuals: T_{pref} ($F_{1,69}$=1.57, $P = 0.22$), CT_{max} ($F_{1,65}$=0.67, $P = 0.42$), and CT_{min} ($F_{1,22}$=2.84, $P = 0.11$). We tested for differences in body condition (a measure of plumpness, g/mm) between the populations using a Wilcoxon rank-sum test.

We found that the distribution of preferred temperatures was normal using Shapiro tests, but cold tolerance and heat tolerance were not normally distributed. Thus prior to analyzing selection gradients, we standardized each trait to a mean of zero and unit variance. We tested each standardized trait for normality using q-q plots and Shapiro tests. We found normality for each trait and for the fitness distribution across the pooled datasets, we additionally scaled the values in two ways. We used the values for body size which we scaled as *z*-scores by subtracting the pooled mean and dividing by the standard deviation for each predictor (fitness) and response variable (traits).

We estimated linear selection gradients using regressions. To measure selection (W) on *OSM* (Kingsolver et al. 2001) we assessed the linear relationship (β_i) between the fitness proxy (α) predicted by body size, and the traits CT_{max} and T_{pref} to reveal change independent of other variation (ε) in fitness (Endler 1986). A significant slope, beta β, would indicate that directional selection is occurring in a population based on the fitness of individuals and measured physiological traits (Table 1). We completed an

Table 4. Tests for selection coefficients (β) on three thermal physiology traits in *Ameiva exsul* in populations exposed to mongoose predators or in naïve populations. Significant β for CT_{max} indicates directional selection on that trait. Values of β for preferred body temperature (T_{pref}) and cold tolerance (CT_{min}) were similar between groups. See text for information on use of body size as estimate of fitness.

Trait	**Population**	**β**	**SD**	**F**	***df***	***P***
T_{pref}	Mongoose-exposed	-0.029	0.071	0.16	1,42	0.685
T_{pref}	Naïve	0.117	0.100	1.35	1,28	0.254
CT_{max}	**Mongoose-exposed**	**-0.242**	**0.074**	**10.5 8**	**1,41**	**0.002**
CT_{max}	Naïve	-0.153	0.089	2.95	1,26	0.097
CT_{min}	Mongoose-exposed	0.013	0.071	0.03	1,10	0.862
CT_{min}	Naïve	-0.038	0.028	1.94	1,8	0.200

additional analysis where a linear mixed effects model allowed mongoose presence to vary by population.

Results

We found that individual lizards thermoregulate around narrow temperatures for long periods of time, a behavior rarely recorded for these lizards in the wild. Each lizard held a preferred temperature ± 1.0°C for at least four cloacal readings spanning 20 min. Within the two experimental groups, selected temperatures were significantly higher (W=381, P=0.01) in mongoose-exposed populations (80% T_{pref} *range*: 37.9 – 39.9°C) than in naïve (80% T_{pref} *range*: 37.2 – 38.5 °C) populations. We also found significant shifts in heat tolerance (CT_{max}) observed as significantly higher (W=166, P<0.01) in mongoose-exposed ($\bar{x}$=43.4 range: 42.6°C – 44.2°C) than naïve populations ($\bar{x}$=41.8; range: 40.6°C – 42.7°C). In contrast, cold tolerance (CT_{min}) was similar (W=43, P=0.11) between the two groups (mongoose-exposed range = 16.2 – 25.6 °C; naïve = 15.7 – 27.2 °C). We found no differences in body condition between individuals in the mongoose-exposed and naïve populations (Fig. 12; W=727, P=0.25).

Because of differences in CT_{max}, *OSM* was significantly greater in populations exposed to mongoose than in the naïve populations (W=127, P<0.001; predator- *OSM* mean = 4.5°C; range: 4.3°C – 4.9°C; naïve populations *OSM* mean = 3.8°C; range= 3.7 °C – 4.2°C). As expected, the warming tolerance of the mongoose-exposed and naïve populations did not differ (W=11, P=0.84; t = -0.33, df = 5.03, P=0.75).

Figure 11. We used a replicated field experiment to study the physiological traits of mongoose-exposed (grey line) and naïve (black line) populations. The results of the physiological data collection are shown as smoothed lines fit to the frequency histograms. The maximum critical limit of mongoose-exposed populations diverged significantly from populations naïve to mongoose. Differences in the lower and preferred thermal limits were not significantly different.

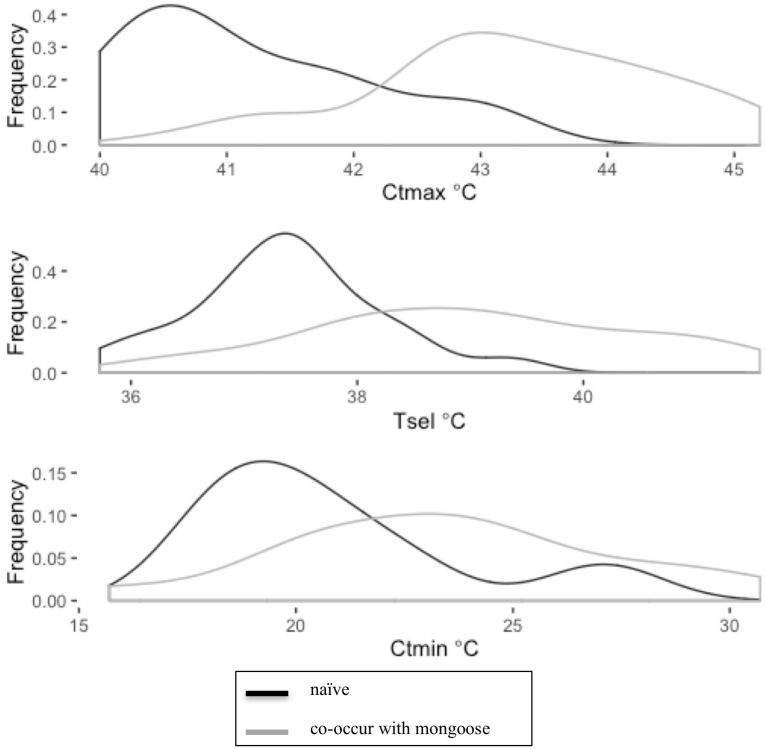
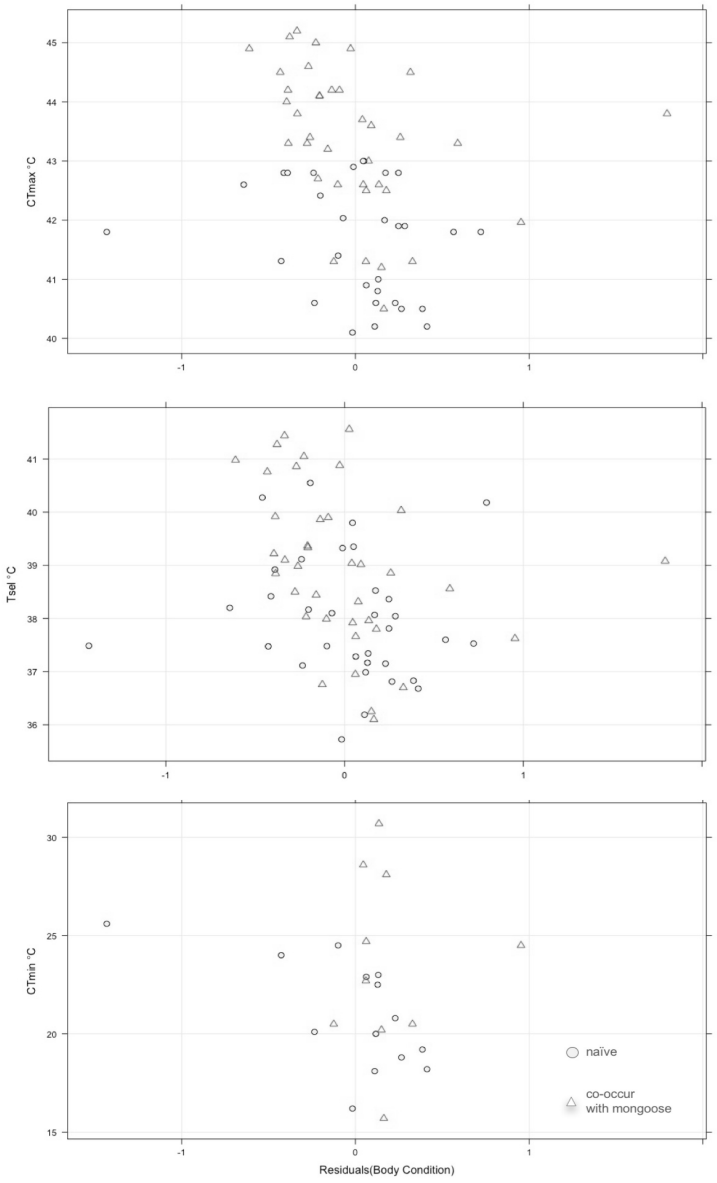


Figure 12. Plumpness as measured by the regression values of the body condition (g/mm) for mongoose-exposed (triangles) individuals as compared to naïve (circles, lightly filled) individuals across all levels within the physiological traits did not differ.



The linear regression resulted in statistically significant, directional selection on heat tolerance (β_{CTmax} = -0.24 ± 0.1) associated with the presence of mongoose. Selection on both cold tolerance and preferred temperature was non-significant (β <0.03, β <0.12, respectively; Table 4). A linear regression with the effects of critical maximum temperature and mongoose presence varying by population fit better than the simple linear regression (χ2=3.52, *P*=0.0001). When mongoose are present, every unit increase in body size decreased the critical maximum temperature by 0.65°C ± 0.50 (t=-1.30). When mongoose were absent, every unit increase of body size decreased critical maximum temperature by 1.39°C ± 1.03 (t=1.35).

No differences in *WT* were observed in in populations based on mongoose exposure (*W*=11*, P = 0.84*; predator *WT* mean = 11.9°C; range: 9.8°C – 12.9°C; naïve populations *WT* mean = 11.7 °C; range= 10.0 °C – 14.2°C). No differences in the thermal safety margin was observed between groups (*W*=17*, P* =0.4; predator *TSM* mean = 7.4°C; range: 5.8°C – 9.7°C; naïve populations *TSM* mean = 8.1°C; range= 6.1 °C – 9.7°C). The results across each population are summarized in Table 5 and individual results in Appendix D.

Discussion

Our analysis revealed that in the presence of a novel predator, ground lizards had higher values of CT_{max}, a measure of heat tolerance. This increase in the upper thermal limits is consistent with the coexistence of lizards with a novel predator. Based on our criteria we could delineate populations of Puerto Rican ground lizards co-occurring with a novel predator, the introduced mongoose and populations that are naïve to the novel

predator. Based on observations of *Ameiva festiva*, Van Berkum et al. (1986) suggested thermal lability of species in the genus *Ameiva* was dependent on sporadic events that impact survival. In our study, we hypothesized that the direct predation by mongoose, resulted in removal of animals with relatively low CT_{max}, resulting in directional selection in heat tolerance, which favored lizards with higher values of CT_{max}. Under this scenario, in populations exposed to mongoose predation, a higher CT_{max} would enable individuals to maintain similar fitness because they could perform better at escaping predation and continue foraging during hot periods. Another possibility is that lizards shifted to using warmer microhabitat increasing heat tolerance, as result consistent with studies in other wild populations (*i.e.,* Angilletta et al. 2007). Our results provide an empirical demonstration in a vertebrate system of one type of biotic interaction that modifies either habitat use or activity period (Hertz et al. 1988) sufficiently to shift thermal tolerance by a rate of 0.73°C for individuals and overall an increase of nearly 2°C between populations in the wild. Further studies of the effects of novel biological interactions on heat tolerance may reveal other conditions where lability in heat tolerance occurs illuminating selection thresholds required for heat tolerance to change.

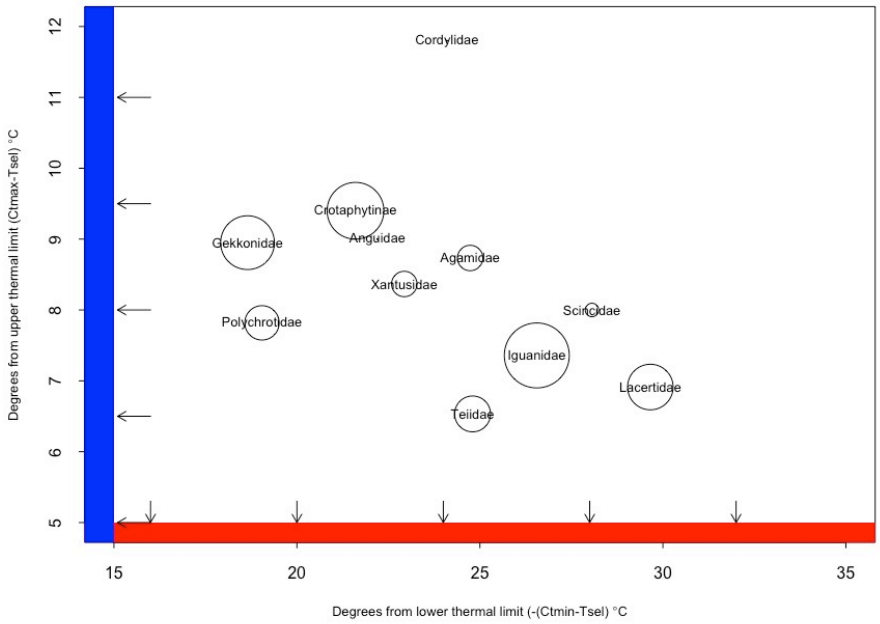
Table 5. Summary of environmental and thermal physiology traits in *Ameiva exsul* in populations exposed to mongoose predators or in naïve populations. The "overheating safety margin" (*OSM*), the difference between CT_{max} and T_{pref} is a measure of the intrinsic tolerance of lizards to overheating, Warming tolerance (*WT)* and thermal safety margin (*TSM*) are reported. Environmental variables including annual rainfall ($T_{env\text{-}pre}$), average temperature of the median month ($T_{env\text{-}avg}$), minimum temperature of the coolest months ($T_{env\text{-}min}$), and maximum temperature of the hottest months ($T_{env\text{-}max}$) are reported.

Population	$T_{env\text{-}max}$	$T_{env\text{-}min}$	$T_{env\text{-}avg}$	$T_{env\text{-}pre}$	*WT*	*TSM*	*OSM*	CT_{max}	CT_{min}	T_{pref}	*Mongoose*
Caja Muertos	31.77	70.00	79.00	49.07	-10.05	-6.05	4.00	40.78	22.60	37.35	N
Culebra	30.00	72.00	80.00	35.00	-12.78	-9.38	3.40	41.79	20.08	37.30	N
Culebrita	30.00	72.00	80.00	56.38	-10.78	-7.35	3.43	40.95	18.49	36.94	N
Borinquen	30.39	70.70	78.70	52.00	-10.98	-7.78	3.20	42.78	23.20	39.38	N
Cidra	27.61	64.70	73.20	52.00	-14.18	-9.69	4.49	41.37	_	38.17	N
Arecibo	31.11	67.90	78.00	51.02	-9.84	-5.83	4.01	41.82	22.01	37.82	Y
Dos Bocas	30.78	67.50	77.50	74.61	-12.94	-7.69	5.25	43.72	_	38.47	Y
Lajas	31.67	65.80	77.50	45.01	-12.55	-6.77	5.78	44.22	22.33	38.44	Y
Mayaguez	31.50	67.70	78.20	68.66	-11.62	-7.25	4.37	43.12	_	38.75	Y
Vieques	31.00	69.50	78.60	42.00	-12.80	-9.67	3.13	43.80	20.31	40.67	Y

The benefits of lability in CT_{max} and a broader *OSM* on survival and reproduction is presumably high. We considered selection to be strong if it was greater than the median $|\beta| = 0.16$ (Hoekstra et al. 2001). Only selection on CT_{max} was strong. Benefits of thermal acclimation and adaptation to alleviate stress in future generations are an expected benefit of adaptation on thermal tolerance (Buckley and Huey 2016). Mongoose-exposed lizards may have regained losses in fitness associated with shifts in habitat use, activity period, or direct predator evasion when the mongoose was first introduced nearly a century ago (Fig. 11).

The stasis of heat tolerance is observed in studies of abiotic factors like climate and geography. Low capacity for change in thermal tolerance could inhibit the evolution of adaptive traits for species facing global change (Gunderson and Stillman 2015). Many ectotherms, in particular, species with high metabolic rates and high locomotor activity tend to thermoregulate at high body temperatures (Angilletta et al. 2007, Kingsolver and Huey 1989). While there are presumably limits on evolution of thermal tolerance (Santos et al. 2012, Klok et al. 2004, Bullock 1955), the ability of species to respond physiologically to heat stress may be one way for species to persist in a changing world. We provided evidence that exposure novel predators probably caused an upward shift in CT_{max} and a broader *OSM* as a result of increased heat stress affecting which individuals could contribute to future generations.

Figure 13. Lizards thermoregulate (T_{sel}) closer to either their upper or lower thermal limit. Among the lizard families, the Lacertids and Teiids thermoregulate most closely to their upper thermal limit, while the Gekkonids and Polychrotids thermoregulate more closely to their lower thermal limit. Circles correspond to sample size of species (range: 1 – 11). The arrows show the direction of the critical maximum (red) and critical minimum thermal limits, i.e. the closer the point is to the boundary, the closer the family optimally thermoregulates to a critical thermal limit. The data are compiled from 72 studies of reptile species in 10 taxonomic families. Data from Martin and Huey (2008), Huey et al. 2012, Angilletta 2009, and this study.



Further investigations into the intrinsic capacity of species to adapt to novel co-occurring species, communities, and climate can benefit from considering the *OSM* we used. Among lizards, body size, habitat affinity, or life history traits, or phylogenetic constraints on physiological attributes may mediate the capacity for shifts in *OSM* (Fig. 13; Martin and Huey 2008, Angilletta 2009, Huey et al., 2009). It is plausible the *OSM* may have played a role in historic declines in some species. As an example, it is enigmatic that in the Caribbean some, but not all teiids, are resilient to predation from mongoose (Henderson 1992). While Puerto Rican ground lizards (*Ameiva exsul)* persist with mongoose, this predator was responsible for the near extinction of St. Croix ground lizards (*Ameiva polops)* and a number of other lizards and snakes (Henderson 1992). Further research may reveal important variance in lability of thermal tolerance in this group of lizards, among closely related species, and help explain why some teiids are more susceptible to invasive predators than others. Some puzzling declines unrelated to island size, prey base, or predator base may be solved by a deeper understanding of species physiological capacities.

CHAPTER V

SUMMARY AND CONCLUSION

"*All successful animals must remain functionally integrated...By focusing questions on these obligatory and universal capacities, one can ensure that one's research will not be trivial and will have some chance of achieving general significance."* George Bartholomew (1987).

The central question that I asked in my dissertation was: Why do some species of ground lizards persist while others have gone extinct? I sought to conduct research that could lead to new approaches for the conservation of species on islands. I predicted that the synthesis of biological data into mechanistic models could lead to a more complete understanding of why some species persist and in what places. I found that the decline of St. Croix ground lizards but not Puerto Rican ground lizards may be mediated by thermoregulation that was labile for the more widespread Puerto Rican ground lizard. Using thermoregulation to predict the effects of future change in the landscape and interspecific species interactions is appropriate for ground lizards. Yet conservation actions for species based on their thermoregulation today will need to be sought to inform the persistence of species in the future because the world is rapidly changing. Fine-scale components of the landscape will continue to change based on continual development and inputs, and species will need to adjust to threats continuously.

Specifically, I investigated the distribution and population growth of a recently translocated population of St. Croix ground lizards to Buck Island, St. Croix, a small island administered by the National Park Service and collaboratively investigated. I used

information on thermally suitable areas and the intrinsic biology of the species to identify how the lizard associates with available environmental variables. The resulting dataset informed the mechanistic model to predict habitat on the larger island of St. Croix. We identified 195 ha of land on St. Croix suitable for ground lizards.

Novel landscapes present new opportunities for repatriation of species. Based on the following lines of evidence, we are suggesting repatriation of the lizard to St. Croix. First, the island of St. Croix is beginning to form in historic proportions of habitat cover, potential refugia for the St. Croix ground lizard. Second, the distribution of threats on the landscape of St. Croix has changed. Mongoose have always been patchy, and today the threat posed by predation is recognized allowing the proliferation of control programs. Lastly, opportunities exist for local stakeholders to contribute to species recovery, including local tourism ventures by supporting repatriation efforts. To that end, I have written a complement to dissertation chapter II, a 2^{nd} – 4^{th} grade level children's book called the Lizard Lady (Angeli et al. 2018). Telling our children about the on-going work of conservation biology is an important step for garnering support for species conservation.

The repatriation approach for species recovery in this dissertation is meant to be applied in St. Croix and inspire strategies for species recovery across the Caribbean. The pernicious threat of mongoose predation in the Caribbean persists despite years of conservation action (Doremus and Pagel 2001, Doak et al. 2015). Other endangered species in the Caribbean are similarly restricted as *Ameiva polops* to uninhabited offshore islands, including *Cyclura stejnegeri* (García et al. 2016) and *Chilabothrus*

granti (Reynolds et al. 2015) in the Puerto Rican land bank. Local conservation biologists can repatriate species in some cases today. Demonstrating feasibility of re-introducing species' where threats still exist should be a conservation priority. A challenge for conservation biologists is to find which lines of evidence are required for species assessments and of the landscapes of threats of today.

Implications for Conservation

The Applied Biodiversity Sciences program promotes the integration of research and conservation outcomes. As a student and participant in the Applied Biodiversity Sciences program, I conducted research in collaboration with local institutions, with an aim towards achieving broader impacts for conservation of ground lizards in the Caribbean. Working with local governmental, business, and non-profit stakeholders, I helped conservation practitioners determine that protected land exists on St. Croix and repatriating the St. Croix ground lizard is the next course of action. Together, we identified 8 recommendations in Oct 2014 to aid in the recovery of the St. Croix ground lizard. Three suggestions were specifically related to repatriation, and five were related to the protection of the offshore populations (Table 6).

Table 6. Recommendations for the recovery of the St. Croix ground lizard created with managers and stakeholders with the knowledge generated from this doctoral dissertation.

Recommendations
A. Establishing New Populations
1. The Working Group recommends that repatriation efforts can begin as early as 2015. Agency collaborations are in place, appropriate sites are being identified, and action steps are being formulated. The conservation needs for *A. polops* are imminent.
2. Repatriation is possible on mainland St. Croix due to land use changes, including conservation and restoration actions that are different from historic conditions. Repatriating *A. polops* to St. Croix should be attempted to demonstrate the feasibility of establishing populations on mainland St. Croix. Repatriation sites need to be secure in terms of land tenure and land use, have low predicted levels of predation where predators can be controlled, and contain suitable habitat for *A. polops*.

Table 6. Continued

Recommendations
3. Long term protection of the lizard, if repatriated, will require programs designed to control exotic predators. Programs include building capacity to guard against introduction of exotics, educating stakeholders, and partnerships with agencies having predator management authority. Potential sites for future population could be fenced to exclude mongoose, including Sandy Point National Wildlife Refuge, East End Marine Park, and Salt River Bay National Historic Park and Ecological Preserve.

Table 6. Continued

Recommendations
B. Protecting Current Populations
4. All populations need to be regularly monitored. Populations should be monitored with standardized methodology that provides information to estimate occupancy, population structure, and abundance. The National Park Service contracted and completed a Standard Operating Procedure ("St. Croix ground lizard Monitoring Protocol") in 2014 that could be adopted by management agencies and researchers.
5. Reciprocal translocations to maintain diversity between populations on Ruth and Protestant Cays, and Green Cay and Buck Island should occur. Transfer of approximately 10 lizards every decade between the replicate populations will maintain the long-term genetic integrity of the species. The Working Group recommends consultation with a conservation geneticist each decade.
6. The habitat requirements for *A. polops* are more general than previously thought, and we now know that the species uses a variety of vegetation communities in sandy and rocky soils ranging from canopy forests to shrublands to landscape plantings and edge debris. The main requirement for the species is habitat structure that creates a mosaic of open and shaded patches, ample leaf litter, and appropriate refugia.

Table 6. Continued

Recommendations
7. Efforts to improve habitat should continue for existing populations. Site-specific actions should be evaluated by an ecologist and could include removal of invasive vegetation that creates unsuitable habitat (complete shade), planting of suitable native trees and shrubs (Lantana involucrata, Tabebuia heterophylla, Conocarpus erectus and others) that break up the soil and provide protection from aerial predators to encourage lizard burrowing and foraging, and rat eradiation/control to diminish probable predation on lizard eggs and juveniles.
8. Ameiva exsul, a large lizard from Puerto Rican Bank islands, has invaded St. Croix and should be eradicated to reduce chances of competitive interactions between *A. polops* and other native fauna. *Ameiva polops* has never occurred with *A. exsul* and may be susceptible to predation from *A. exsul* which is known to consume other lizards. *Ameiva exsul* may displace *A. polops* or impede colonization of areas by *A. polops*. The potential impacts of competitive displacement and priority effects caused by *A. exsul* should be addressed.

Recovery actions can use mechanistic models to identify where species are vulnerable to predators and where they may persist despite the presence of predators. The introduction of mammalian predators has disrupted native species assemblages and caused many extinctions worldwide (Blackburn et al. 2004, Pitt and Witmer 2007). Programs established to control predators have had mixed success (for example, Treves et al. 2016, Garnett 2012, King et al. 2009, Walsh et al. 2012). Thus, identifying how to conserve species where threats still exist is necessary goal for conservation practitioners and a contribution of this dissertation to the academic community of applied biodiversity sciences.

In short, I investigated biodiversity conservation, which is broadly the sum of ecosystems, communities, species, and genes, all which have co-evolved throughout history. The relative contribution of each organism is in a delicate balance. Conserving species where they exist and have existed in the past based on current landscapes and new interactions is important work for conservation of species in the field of biodiversity conservation sciences. The doctoral dissertation presented here is a small contribution to the state of knowledge and ideas in biodiversity conservation. The efforts herein to recover a single species are a critical component of averting a new extinction. By asking how '*successful animals remain functionally integrated'*, I use biologically relevant information to make conservation recommendations for a relatively unsuccessful animal (Bartholomew 1987). The optimistic message of repatriation broadens species-specific goals to stimulate conservation actions to preserve species in the future.

REFERENCES

Alexander JM, Diez JM, Levine, JM. 2015. Novel competitors shape species' responses to climate change. Nature 525: 515 – 520.

Angeli NF, Keats Curtis J, Jones V. 2018 (In Press). The lizard lady. Arbordale Publishing, Mount Pleasant, South Carolina. 31 pp.

Angeli NF, Lundgren IF, Pollock C, Hillis-Starr Z, Fitzgerald LA. 2017. (In Press). Dispersal and population state of an endangered island lizard following a conservation translocation. Ecological Applications.

Angilletta MJ, Wilson RS, Niehaus AC, Sears MW, Navas CA, Ribeiro PL. 2007. Urban physiology: city ants possess high heat tolerance. PLoS One 2: e258.

Angilletta MJ. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press.

Angilletta MJ, Niewiarowski PH, Navas CA. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27: 249 – 268.

Atkinson E, Marín-Spiotta E. 2015. Land use legacy effects on structure and composition of subtropical dry forest in St. Croix, U.S. Virgin Islands. Forest Ecology and Management 33: 270 – 280.

Attum O, Cutshall C, Eberly K, Day H, Tietjen B. 2013. Is there really no place like home? Movement, site fidelity, and survival probability of translocated and resident turtles. Biodiversity and Conservation 22: 3185 – 3195.

Bakken G, Angilletta M. 2013. How to avoid errors when quantifying thermal environments. Functional Ecology 28: 96 – 107.

Bakken GS. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32: 94 – 216.

Bartholomew GA. 1987. Interspecific comparison as a tool for ecological physiologists. Pp. 11 – 37. In: Feder ME, Bennet AF, Burggren WW, Huey RB (eds.) New Directions in Ecological Physiology. Cambridge University Press, New York. 365 pp.

Barton, K. 2013. MuMIn: Multi-model inference. <http://CRAN.R-project.org/package=MuMIn>.

Barun A, Hanson CC, Campbell KJ, Simberloff D (2011) A review of small Indian mongoose management and eradications on islands. Island invasives: eradication and management. IUCN, Gland, Switzerland, pp 17 – 25.

Bastille-Rousseau G, Potts J, Yackulic C, Frair J, Ellington E, Blake S. 2016a. Flexible characterization of animal movement pattern using net squared displacement and a latent state model. Movement Ecology 4: 1 – 12.

Bastille-Rousseau G, Schaefer JA, Lewis KP, Mumma MA, Ellington EH, Rayl ND, Mahoney SP, Pouliot D, Murray DL. 2016b. Phase-dependent climate–predator interactions explain three decades of variation in neonatal caribou survival. Journal of Animal Ecology 85: 445 – 456.

Bennett NL, Severns PM, Parmesan C, Singer MC. 2015. Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. Oikos 124: 41 – 53.

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955 – 1958.

Bled F, Sauer J, Pardieck K, Doherty P, Royle J. 2013. Modeling trends from North American Breeding Bird Survey Data: A spatially explicit approach. PLosONE 8: e81867.

Blows MW, Hoffmann AA. 2005. A reassessment of genetic limits to evolutionary change. Ecology 86: 1371 – 1384.

Boulangeat I, Gravel D, Thuiller W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters 15: 584 – 593.

Bowden M. 1968. Water balance of a dry island. Geograph. Publ. Dartmouth 6: 1 – 89.

Braun-Blanquet, J. 1932. Plant sociology (Translated by G. D. Fuller and H. S. Conrad). McGraw-Hill, New York. 539 pp.

Brook BW, Sodhi NS, Bradshaw CJ. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23: 453 – 460.

Brown S. Lugo AE. 1990. Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico and US Virgin Islands. Plant and Soil 124: 53 – 64.

Buckland S, Cole N, Aguirre-Gutierrez J, Gallagher L, Henshaw S, Besbard A, Tucker R, Bachraz V, Ruhomaun K, Harris S. 2014. Ecological effects of the invasive giant Madagascar Day Gecko on endemic Mauritian Geckos: applications of binomial-mixture and species distribution models. PlosOne 9: e88798.

Buckley LB, Huey RB. 2016. Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities. Global Change Biology 22: 3829 – 3842.

Buckley LB. 2010. The range implications of lizard traits in changing environments. Global Ecology and Biogeography 19: 452 – 464.

Bullock TH. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. Biological Reviews 30: 311 – 342.

Carroll C, Rohlf DJ, Li YW, Hartl B, Phillips MK, Noss RF. 2015. Connectivity conservation and endangered species recovery: a study in the challenges of defining conservation-reliant species. Conservation Letters 8: 132 – 138.

Case JE, Holcombe TL. 1980. Geologic-tectonic map of the Caribbean region 1100. U.S Geological Survey Miscellaneous Investigations Series Map I-1100, scale 1:2,500,000. Prepared in cooperation with the United States Naval Oceanographic Office and the United States Naval Ocean Research and Development Activity.

Chapron G, Kaczensky P, Linnell JD, Von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O, Balčiauskas L.2014. Recovery of large

carnivores in Europe's modern human-dominated landscapes. Science 346:1517 – 1519.

Chevin LM, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol 8: e1000357.

Chiang PJ, Pei KJC, Vaughan MR, Li CF, Chen MT, Liu JN, Lin CY, Lin LK, Lai YC. 2015. Is the clouded leopard *Neofelis nebulosa* extinct in Taiwan, and could it be reintroduced? An assessment of prey and habitat. Oryx 49:261 – 269.

Clusella-Trullas S, Blackburn TM, Chown SL. 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. The American Naturalist 177: 738 – 751.

Cohen J. 1988. Statistical power analysis for the behavioral sciences. 2nd edition. Hillsdale, NJ: Erlbaum.

Cohen J. 1992. A power primer. Psychological Bulletin 112: 155.

Connette GM, Semlitsch RD. 2013. Life history as a predictor of salamander recovery rate from timber harvest in southern Appalachian forests, USA. Conservation Biology 27:1399 – 1409.

Courchamp F, Chapuis JL, Pascal M. 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347 – 383.

Crother B I. (ed). 1999. Caribbean Amphibians and Reptiles. Academic Press.

Cruz FB, Fitzgerald LA, Espinoza RE, Schulte JA. II. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a

clade of South American lizards. Journal of Evolutionary Biology 18:1559 – 1574.

Davidson A, Carmel Y, Bar-David S. 2013. Characterizing wild ass pathways using a non-invasive approach: applying least-cost path modelling to guide field surveys and a model selection analysis. Landscape Ecology 28: 1465 – 1478.

Davis J. 2002. Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic SSURGO Database for Virgin Islands of the United States. Available online at http://soildatamart.nrcs.usda.gov. Accessed 09/24/2013.

Dawson J, Oppel S, Cuthbert RJ, Holmes N, Bird JP, Butchart SH, Spatz DR, Tershy B. 2015. Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. Conservation Biology 29:143 – 153.

Debeaudette D. 2009. Aggregating SSURGO Data in R. California Soil Resource Lab.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105: 6668 – 6672.

Diamond SE. 2016. Evolutionary potential of upper thermal tolerance: biogeographic patterns and expectations under climate change. Annals of the New York Academy of Sciences 1389: 5–19.

Dickinson H, Fa J, Lenton S. 2001. Microhabitat use by a translocated population of St. Lucia whiptail lizards *Cnemidophorus vanzoi*. Journal of Zoology 251: 187 – 197.

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution 22:489 – 496.

Doak DF, Bakker VJ, Goldstein BE, Hale B. 2015. What is the future of conservation? In: Protecting the Wild (pp. 27 – 35). Island Press/Center for Resource Economics.

Dodd CK. 1978. Island lizard in danger. National Parks Conservation Magazine 52:10 – 11.

Dodd CK. 1980. *Ameiva polops* (Cope). St. Croix Ground lizard. Catalogue of American Amphibians and Reptiles 240:1 – 2.

Doherty TS, Dickman CR, Nimmo DG, Ritchie EG. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biological Conservation 190:60 – 68.

Doremus H, Pagel JE. 2001. Why listing may be forever: perspectives on delisting under the US Endangered Species Act. Conservation Biology 15:1258 – 1268.

Dzialowski E. 2005. Use of operative temperature and standard operative temperature models in thermal biology. Journal of Thermal Biology 30:317 – 334.

Earnhardt J, Vélez-Valentín J, Valentin R, Long S, Lynch C, Schowe K. 2014. The Puerto Rican Parrot reintroduction program: sustainable management of the aviary population. Zoo Biology 33:89 – 98.

Elton C. 1927. The nature and origin of soil-polygons in Spitsbergen. Quarterly Journal of the Geological Society 83:1 – 7.

Endler JA. 1986. Natural selection in the wild. Princeton University Press, 354 pp.

Fiske IJ, Chandler RB. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software 43:1 – 23.

Fitzgerald LA, Stronza A. 2009. Applied biodiversity science: bridging ecology, culture, and governance for effective conservation. Interciencia 34:563 – 570.

Fitzgerald LA, Treglia M, Angeli NF, Hibbitts T, Leavitt D, Subalusky A, Lundgren IF, Hillis-Starr Z. 2015. Determinants of successful establishment and post-translocation dispersal of a new population of the critically endangered St. Croix ground lizard (*Ameiva polops*). Restoration Ecology 23:776 – 786.

Fitzgerald L, Walkup D, Chyn K, Buchholtz E, Angeli NF, Parker M. The future for reptiles: advances and challenges in the Anthropocene. In: D. DellaSala and M. Goldstein (eds.). Accepted. 2017. Encyclopedia of the Anthropocene.

García M, Gerber GP. 2016. Conservation and management of Cyclura iguanas in Puerto Rico. Herpetological Conservation and Biology 11:61 – 67.

Garnett ST. 2012. Unexpected outcomes of invasive predator control. Animal Conservation 15:329 – 330.

Gasc A, Duryea MC, Cox RM, Kern A, Calsbeek R. 2010. Invasive predators deplete genetic diversity of island lizards. PloS One 5:e12061.

Germano JM, Field KJ, Griffiths RA, Clulow S, Foster J, Harding G, Swaisgood RR. 2015. Mitigation-driven translocations: are we moving wildlife in the right direction? Frontiers in Ecology and the Environment 13:100 – 105.

Gesch, D. 2007. The National Elevation Dataset. Pp. 99 – 118. *In* Maune, D. (ed.), Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition: Bethesda, Maryland, American Society for Photogrammetry and Remote Sensing.

Gifford ME, Clay TA, Powell R. 2012. Habitat use and activity influence thermoregulation in a tropical lizard, *Ameiva exsul*. Journal of Thermal Biology 37: 496 – 501.

Gould WA. (ed.) 2007. The Puerto Rico Gap Analysis Project. USDA Forest Service, International Institute of Tropical Forestry General Technical Report IITF – GTR – 39, San Juan, Puerto Rico.

Gunderson AR, Stillman JH. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proceedings of the Royal Society of London B: Biological Sciences 282: e20150401.

Hays WS, Conant S. 2007. A worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora: Herpestidae). Pacific Science 61:3 – 16.

Henderson RW. 1992. Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. Caribbean Journal of Science 28:1 – 10.

Hertz P, Huey R, Stevenson R. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. American Naturalist 145: 796 – 818.

Hertz PE, Huey RB, Garland T. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts?.American Zoologist 28: 927 – 938.

Hoagland DB, Horst GR, Kilpatrick CW. 1989. Biogeography and population biology of the mongoose in the West Indies. Biogeography of the West Indies: 611 – 634.

Hoare JM, Adams LK, Bull LS, Towns DR. 2007. Attempting to manage complex predator–prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. Journal of Wildlife Management 71: 1576 – 1584.

Hobbs RJ, Higgs E, Harris JA. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24: 599 – 605.

Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hoang A, Hill CE, Beerli P, Kingsolver JG. 2001. Strength and tempo of directional selection in the wild. Proceedings of the National Academy of Sciences 98: 9157 – 9160.

Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? Functional Ecology 27: 934 – 949.

Hopkins D. 1989. An extraordinary eighteenth-century map of the Danish sugar-plantation island St. Croix. Imago Mundi 41:44 – 58.

Horst GR, Hoagland DB, Kilpatrick CW. 2001. The mongoose in the West Indies: the biogeography and population biology of an introduced species. pp: 409 – 424. In: Woods CA and Sergile FE (eds.) Biogeography of the West Indies: Patterns and Perspectives 2. CRC Press.

Huey R, Kingsolver JG. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution 4: 131 – 135.

Huey R, Deutsch C, Tewksbury J, Vitt L, Hertz P, Pérez H, Garland T. 2009. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society of London B: Biological Sciences 276: 1939 – 1948.

Huey RB, Hertz PE, Sinervo B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. The American Naturalist 161: 357 – 366.

Hurtado L, Santamaria C, Fitzgerald L. 2012. Conservation genetics of the critically endangered St. Croix ground lizard (*Ameiva polops* Cope 1863). Conservation Genetics 13: 665 – 679.

Jakob E, Marshall S, Uetz G. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77: 61 – 67.

Joseph L, Field S, Wilcox C, Possingham H. 2006. Presence–Absence versus Abundance Data for Monitoring Threatened Species. Conservation Biology 20: 1679 – 1687.

Karlin M, Vaclavik T, Chadwick J, Meentemeyer R. 2016. Habitat use by adult red wolves, *Canis rufus*, in an agricultural landscape, North Carolina, USA. Mammal Study 41: 87 – 95.

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334 – 350.

Kearney M, Prevadec M. 2000. Do nocturnal ectotherms thermoregulate? A study of the temperature gecko *Christinus marmoratus.* Ecology 81:2984 – 2996.

Kendall W. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. Ecology 90:2517 – 2525.

Kéry M, Royle J. 2010. Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. Journal of Animal Ecology 79:453 – 461.

Kéry M, Royle J, Schmid H. 2005. Modeling avian abundance from replicated counts using *N*-mixture models. Ecological Applications 15:1450 – 1461.

King CM, McDonald RM, Martin RD, Dennis T. 2009. Why is eradication of invasive mustelids so difficult? Biological Conservation 142:806 – 816.

Kingsolver JG, Huey RB. 1998. Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. American Zoologist 38:545 – 560.

Kingsolver JG, Pfennig DW. 2007. Patterns and power of phenotypic selection in nature. Bioscience 57:561 – 572.

Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang, A, Gibert P, Beerli P. 2001. The strength of phenotypic selection in natural populations. The American Naturalist 157:245 – 261.

Klok CJ, Sinclair BJ, Chown SL. 2004. Upper thermal tolerance and oxygen limitation in terrestrial arthropods. Journal of Experimental Biology 207: 2361 – 2370.

Knape J, Korner-Nievergelt F. 2016. On assumptions behind estimates of abundance from counts at multiple sites. Methods in Ecology and Evolution 7: 206 – 209.

Kolbe JJ, Van Middlesworth PS, Losin N, Dappen N, Losos JB. 2012. Climatic niche shift predicts thermal trait response in one but not both introductions of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, USA. Ecology and Evolution 2:1503 – 1516.

Krebs C. 2014. Ecological Methodology, 3rd ed. Addison – Wesley Longman, Inc., Menlo Park, California. 744 pp.

Leal M, Gunderson AR. 2012. Rapid change in the thermal tolerance of a tropical lizard. The American Naturalist 180:815 – 822.

Lewis AR, Tirado G, Sepulveda, J. 2000. Body size and paternity in a teiid lizard *Ameiva exsul*. Journal of Herpetology 34:110 – 120.

Lewis DS, van Veen R, Wilson BS. 2011. Conservation implications of small Indian mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica. Biological Invasions 13:25 – 33.

Lewis AR, Salvia JE. 1987. Effects of sex and size on home range, dominance, and activity budgets in *Ameiva exsul* (Lacertilia: Teiidae). Herpetologica 374 – 383.

Logan ML, Cox RM, Calsbeek R. 2014. Natural selection on thermal performance in a novel thermal environment. Proceedings of the National Academy of Sciences 111:14165 – 14169.

Lutterschmidt W, Hutchinson V. 1997. The critical maximum: history and critique. Canadian Journal of Zoology 75:1561 – 1574.

MacKenzie D, Nichols J, Royle JA, Pollock K, Bailey L, Hines J. 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press (Elsevier), San Diego, California. 324 pp.

Manne LL, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands. Nature 399:258– 261.

Martin TL, Huey RB. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. The American Naturalist 171: E102– E118.

Mazzerolle M, Bailey L, Kendall W, Royle JA, Converse S, Nichols J. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672– 689.

McCune B, Grace J. 2002. Analysis of ecological communities. Vol. 28. Gleneden Beach, Oregon: MjM software design. 304 pp.

McDonald RI, Boucher TM. 2011. Global development and the future of the protected area strategy. Biological Conservation 144:383 – 392.

McNair D, Lombard C. 2004. Population estimates, habitat associations, and management of *Ameiva polops* (Cope) at Green Cay, United States Virgin Islands. Caribbean Journal of Science 40:353 – 361.

Meier AJ, Noble RE, Zwank PJ. 1990. Criteria for the introduction of the St. Croix ground lizard. New York State Museum Bulletin 471:154 – 156.

Meier A, Noble R, Rathburn S. 1993. Population status and notes on the biology and behavior of the St. Croix ground lizard on Green Cay (St. Croix USVI). Caribbean Journal of Science 29:147 – 152.

Meot A, Legendre P, Borcard D. 1998. Partialling out the spatial component of ecological variation: questions and propositions in the linear modelling framework. Environmental and Ecological Statistics 5:1 – 27.

Milanovich J, Hocking D, Peterman W, Crawford J. 2015. Effective use of trails for assessing terrestrial salamander abundance and detection: A case study at Great Smoky Mountains National Park. Natural Areas Journal 35:590 – 598.

Moser J, Whelan K, Shamblin R, Atkinson A, Patterson J. 2010. Buck Island Reef National Monument, U.S. Virgin Islands, Vegetation Mapping Project 2009. Natural Resource Technical Report. NPS/SFCN/NRTR – 2010/293. National Park Service, Fort Collins, Colorado. 25 pp.

Nellis DW, Everard COR. 1983. The biology of the mongoose in the Caribbean. Studies on the fauna of Curacao and other Caribbean Islands 64:1– 162.

Nellis DW, McManus JJ. 1974. Thermal tolerance of the mongoose, *Herpestes auropunctatus*. Journal of Mammalogy 55:645– 647.

Norton D, Young L, Clarkson B. 2016. Introduction to special section on New Zealand restoration. Ecological Management & Restoration 17:168 – 169.

Ostendorf B, Boardman WS, Taggart DA. 2016. Islands as refuges for threatened species: multispecies translocation and evidence of species interactions four decades on. Australian Mammalogy 38:204 – 212.

Overgaard J, Kristensen TN, Mitchell KA, Hoffmann AA. 2011. Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? The American Naturalist 178:80–96.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37:637–669.

Pech R, Maitland M. 2016. Conservation of native fauna in highly invaded systems: managing mammalian predators in New Zealand. Restoration Ecology 24:816 – 820.

Philibosian R, Yntema J. 1976. Records and status of some reptiles and amphibians in the Virgin Islands: 1968 – 1975. Herpetologica 32:81 – 85.

Philibosian R, Ruibal R. 1971. Conservation of the lizard *Ameiva polops* in the Virgin Islands. Herpetologica 27:450 – 454.

Phillips BL, Shine R. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proceedings of the National Academy of Sciences of the United States of America 101:1715 – 17155.

Pitt W, Witmer G. 2007 Invasive predators: a synthesis of the past, present, and future. In: A. Elewa (ed.) Predation in organisms: a distinct phenomenon, Springer-Verlag, Berlin. pp. 265– 293.

Powell R, Henderson RW. 2012. Island lists of West Indian amphibians and reptiles. Florida Museum of Natural History, University of Florida. Gainsville, Florida.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B: Biological Sciences 267:1947– 1952.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18:1725–1737.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, url: http://www.R-project.org.

Reynolds RG, Puente-Rolón AR, Platenberg R, Tyler RK, Tolson PJ, Revell LJ. 2015. Large divergence and low diversity suggest genetically informed conservation strategies for the endangered Virgin Islands boa (*Chilabothrus monensis*). Global Ecology and Conservation 3:487 – 502.

Rivera-Milán FF, Boomer GS, Martínez AJ. 2016. Sustainability assessment of Plain Pigeons and White-crowned Pigeons illegally hunted in Puerto Rico. The Condor 118:300 – 308.

Rivero JA, 1998. Amphibians and Reptiles of Puerto Rico. La Editorial, UPR.

Rodda G, Campbell E, Fritts R, Clark C. 2005. The predictive power of visual searching. Herpetological Review 36:259 – 264.

Rodda G, Dean-Bradley K, Campbell E, Fritts T, Lardner B, Adams A, Reed R. 2015. Stability of detectability over 17 years at a single site and other lizard detection comparisons from Guam. Journal of Herpetology 49: 513– 521.

Rodriguez-Ramirez J, Lewis AR. 1991. Reproduction in the Puerto Rican teiids *Ameiva exsul* and *A. wetmorei*. Herpetologica 1991: 395– 403.

Royle JA. 2004. *N*-mixture models for estimating population size from spatially replicated counts. Biometrics 60: 108– 115.

Royle J, Nichols J. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84: 777– 790.

Royle J, Dorazio R. 2008. Hierarchical modeling and inference in ecology. Academic Press, California, USA. 444 pp.

Russell JC, Innes JG, Brown PH, Byrom AE. KG. 2015. Predator-Free New Zealand: Conservation Country. BioScience 65: 520– 525.

Santos M, Castañeda LE, Rezende EL. 2012. Keeping pace with climate change: what is wrong with the evolutionary potential of upper thermal limits? Ecology and Evolution 2: 2866 – 2880.

Sax DF, Gaines SD. 2008. Species invasions and extinction: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences 105: 11490 – 11497.

Schmidt J, Johnson D, Lindberg M, Adams L. 2015. Estimating demographic parameters using a combination of known-fate and open *N*-mixture models. Ecology 96: 2583 – 2589.

Seaman GA. 1952. The mongoose and Caribbean wildlife. Trans. North American Wildlife Conference 17:188 – 197.

Seaman GA, Randall J. 1962. The Mongoose as a Predator in the Virgin Islands. Journal of Mammalogy 43: 544 – 546.

Sears M, Angilletta M. 2015. Costs and Benefits of Thermoregulation Revisited: Both the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs. American Naturalist 185: E94 – E102.

Sears MW, Angilletta MJ. 2015. Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. The American Naturalist 185: E94 – E102.

Seddon P, Strauss WM, Innes J. 2012. Animal Translocations: What Are They and Why Do We Do Them? Pp. 1 – 32. In: Ewen, J., D. Armstrong, K. Parker, and P. Seddon (ed.), Reintroduction Biology: Integrating Science and Management: Wiley-Blackwell, Oxford. xxv + 499 pp.

Seebacher F, Franklin CE. 2012. Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. Philosophical Transactions of the Royal Society of London B: Biological Sciences 367: 1607 – 1614.

Seebacher F. 2005. A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? Journal of Comparative Physiology B 175: 453 – 461.

Sexton J, McIntyre P, Anger A, Rice K. 2009. Evolution and Ecology of Species Range Limits. Annual Review of Ecology, Evolution, and Systematics 40: 415 – 436.

Sillett T, Chandler R, Royle J, Kéry M, Morrison S. 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. Ecological Applications 22: 1997 – 2006.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderon-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila LJ, Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Ibarguengoytía N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894 – 899.

Stier AC, Samhouri JF, Novak M, Marshall KN, Ward EJ, Holt RD, Levin PS. 2016. Ecosystem context and historical contingency in apex predator recoveries. Science Advances 2: e1501769.

Sutherland C, Fuller A, Royle J. 2015. Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. Methods in Ecology and Evolution 6: 169 – 177.

Thomas R, Joglar R. 1996. The Herpetology of Puerto Rico. Annals of the New York Academy of Sciences 776:181 – 196.

Treglia M, Fitzgerald LA. 2011. Translocation of the St. Croix ground lizard to Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Pp. 109 – 115. In: Soorae P.S. (Ed.). Global Re-introduction Perspectives: 2011. More case studies from around the globe. Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group and Abu Dhabi, UAE: Environment Agency-Abu Dhabi.

Treves A, Krofel M, McManus J. 2016. Predator control should not be a shot in the dark. Frontiers in Ecology and the Environment 14: 380 – 388.

Tucker DB, Colli GR, Giugliano LG, Hedges SB, Hendry CR, Lemmon EM, Lemmon AR, Sites JW, Pyron RA. 2016. Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae). Molecular Phylogenetics and Evolution 103: 75 – 84.

Tuff KT, Tuff T, Davies KF. 2016. A framework for integrating thermal biology into fragmentation research. Ecology Letters 19: 361 – 374.

Tyson GF. 1992. On the periphery of the peripheries: the cotton plantations of St. Croix, Danish West Indies, 1735-1815. The Journal of Caribbean History 26**:**1 – 36.

U. S. Fish and Wildlife Service. 1984. St. Croix ground lizard Recovery Plan. U.S. Fish and Wildlife Service, Atlanta, Georgia. 26 pp.

U.S. Geological Survey. 2013. Earth Resources Observation & Science Center, United States Department of Interior. Landsat 8 GeoTIFF Data Product for 'LC80030482013139LGN01'. Available online at http://earthexplorer.usgs.gov. Accessed 10/25/2013.

Van Berkum FH, Huey RB, Adams BA, 1986. Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). Physiological Zoology 59: 464 – 472.

Verboom J, Schotman A, Opdam P, Metz J. 1991. European Nuthatch Metapopulations in a Fragmented Agricultural Landscape. Oikos 61: 149 – 156.

Waddle H, Brandt L, Jeffery B, Mazzotti F. 2015. Dry years decrease abundance of alligators in the Florida Everglades. Wetlands 35: 865 – 875.

Walsh JC, Wilson KA, Benshemesh J, Possingham HP. 2012. Unexpected outcomes of invasive predator control: the importance of evaluating conservation management actions. Animal Conservation 15:319 – 328.

Ward S, Rodriguez A, Morgan R. 2000. Estate Thomas Experimental Forest: past, present, and future. In: Zimmerman, T.W. Proceedings of the 5th Annual Caribbean Urban Forestry Conference. UVI, St. Thomas, U.S. Virgin Islands.

Watson J, Whittaker R, Dawson T. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biological Conservation 120: 311 – 327.

Weng Q, Lu D, Schubring J. 2004. Estimation of land surface temperature-vegetation abundance relationship for urban heat island studies. Remote Sensing of Environment 89: 467 – 483.

Westergaard W. 1938. A St. Croix Map of 1766: with a note on its significance in West Indian Plantation Economy. The Journal of Negro History 23: 216 – 228.

Wikelski M, Cooke SJ. 2006. Conservation physiology. Trends in Ecology & Evolution 21: 38 – 46.

Wilcox R. 2011. Modern statistics for the social and behavioral sciences: A practical introduction. CRC press.

Wilder S, Raubenheimer D, Simpson S. 2016. Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. Functional Ecology 30: 108 – 115.

Wiley J. 1984. The ecology and behavior of the St. Croix ground lizard (*Ameiva polops*) an endangered species. Report on file at the Caribbean Island National Wildlife Refuge, Boquerón, Puerto Rico, USA. 35 pp.

Williams N, Hahs A, Morgan J. 2008. A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. Ecological Applications 18: 347 – 359.

Winne CT, Keck MB. 2005. Intraspecific differences in thermal tolerance of the diamondback watersnake (*Nerodia rhombifer*): effects of ontogeny, latitude, and sex. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 140: 141 – 149.

Wintle BA, Bekessy SA, Keith DA, Van Wilgen BW, Cabeza M, Schröder B, Carvalho SB, Falcucci A, Maiorano L, Regan TJ, Rondinini C. 2011. Ecological-economic optimization of biodiversity conservation under climate change. Nature Climate Change 1:355 – 359.

Witmer G, Hillis-Starr Z. 2002. The Eradication of Introduced Rats at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Report to the National Park Service, U.S. Department of the Interior. 67 pp.

Wolf CM, Garland T, Griffith B. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological Conservation 86: 243 – 255.

Yamaura Y, Kéry M, Royle JA. 2016. Study of biological communities subject to imperfect detection: bias and precision of community N-mixture abundance models in small-sample situations. Ecological Research 31: 289 – 305.

Yang D, Song Y, Ma J, Li P, Zhang H, Price MRS, Li C. Jiang Z. 2016. Stepping-stones and dispersal flow: establishment of a meta-population of Milu (*Elaphurus davidianus*) through natural re-wilding. Scientific Reports 6: 27297.

Yott A, Rosatte R, Schaefer J, Hamr J, Fryxell J. 2011. Movement and spread of a founding population of reintroduced elk (*Cervus elaphs*) in Ontario, Canada. Restoration Ecology 19:70 – 77.

Young LC, Van der Werf EA, Lohr MT, Miller CJ, Titmus AJ, Peters D, Wilson L. 2013. Multi-species predator eradication within a predator-proof fence at Ka ‘ena Point, Hawai ‘i. Biological Invasions 15: 2627 – 2638.

Young BE, Stuart SN, Chanson JS, Cox NA, Boucher TM. 2005. Disappearing jewels: the status of new world amphibians. Applied Herpetology 2: 429 – 435.

Zipkin E, Sillett T, Campbell Grant E, Chandler R, Royle J. 2014. Inferences about population dynamics from count data using multistate model: a comparison to capture-recapture approaches. Ecology and Evolution 4: 417 – 426.

APPENDIX A

Table A.1. Because population estimates varied methodologically for the St. Croix ground lizard populations, the estimates cannot be compared across years. [1]Range; other values not given, [2]Mark and recapture; no other details available, [3]Average of 3 estimates: 420, 462 and 421, [4]Mark-resight searches within fixed-width transects, [5]Mean (range); other values calculated from raw data, [6]Counts based on searches within fixed-radii (3 m) points, [7]Maximum (in one-quarter hour), [8]Counts based on searches within an undefined area, [9]Counts based on searches within defined areas.

Population	Year	Number	Method	Source
Green Cay	1967	300	Not given	Philibosian and Ruibal, 1971
	1978	200	Not given	Dodd, 1978
	1981	360 – 4300[1]	Mark and re-sight[2]	USFWS, 1984
	1987	431[3]	Mark re-sight[4]	Meier et al., 1993
	1996	375 (CI: 154 – 564)[5]	Count[6]	Knowles, 1997
	2002	183	Count[9]	McNair and Lombard, 2004

Table A.1. Continued

Population	Year	Number	Method	Source
	2004	1169 – 2177	Count[6]	Mackay, 2007
	2007	576	Count[9]	Mackay, 2007
	2009	413	Mark and re-sight[4]	Treglia and Fitzgerald, 2010
Protestant Cay	1967	200	Not given	Philibosian and Ruibal, 1971
	1978	50 – 100	Not given	Dodd, 1978
	1981	50[1]	Mark and recapture[2]	USFWS, 1984
	1987	29[7]	Count[8]	Zwank, 1987
	1996	23 (CI: 16 – 26)[5]	Count[6]	Knowles, 1997
	2002	30	Count[9]	McNair, 2003
	2003	36	Count[9]	McNair and Coles, 2003
	2009	Sample size too small for analysis	Mark and re-capture[4]	Treglia and Fitzgerald, 2011
	2010	136	Count[9]	Geographic Consulting, 2011

Table A.1. Continued

Population	Year	Number	Method	Source
	2011	249 ± 36	Mark and re-sight[4]	Geographic Consulting, 2011
	2012	129	Count[9]	Geographic Consulting, 2013
	2012	384 ± 47	Mark and re-sight[4]	Geographic Consulting, 2013
Ruth Cay	1995	11	Translocation propagules	McNair and Mackay, 2005
	1996	20	Count[8]	Knowles, 1997
	2002	27	Count[9]	McNair and Mackay, 2005
	2003	60	Count[9]	McNair and Mackay, 2005
	2007	170	Mark and re-sight[4]	Treglia and Fitzgerald, 2010
	2010	Sample size too small for analysis	Count[9]	Geographic Consulting, 2011
	2010		Mark and re-sight[4]	Geographic Consulting, 2011

Table A.1. Continued

Population	Year	Number	Method	Source
Buck Island	2008	57	Translocation propagules	Treglia, 2010
	2013	1,473 (CI: 940 – 1802)	Count	This study

APPENDIX B

Table B.1. Model ranking where abundance (λ) or detection (σ) varied separately used a dispersion parameter (α) in the negative binomial case. Significant covariates used for the final model chosen for a model correcting for both abundance and detection bias. Abbreviations follow as: *k* is number of parameters, *Avg surface* = average soil surface temperature (°C), *Max surface* = maximum temperature on the soil surface (°C), *Avg OTM* = average operative temperature (°C), *Max OTM* = maximum operative temperature (°C); *Dist* = distance from release site (m); *LLd* = leaf litter depth (cm); time = survey hour (categorical); *Woody* = number woody stems; *obs* = observer (categorical); *% Cov* = canopy cover percent; *Hab* = habitat type (categorical).

	k	*AICc*	*w(AIC)*
Abundance Only			
λ(Avg surface+Avg OTM+Dist+LLd+CWD)σ(.)α	*7*	*943.3*	*0.281*
λ(Avg OTM+Dist_Encl+LLd+Woody)σ(.)α	*6*	*943.5*	*0.251*
λ(Avg surface+Avg OTM +Dist+LLd+Max OTM+Woody)σ(.)α	*8*	*945.3*	*0.103*
λ(Dist+LLd+Woody)σ(.)α	*5*	*945.7*	*0.083*
λ(Avg surface+Avg OTM+%Cov+Dist+LLd+Woody)σ(.)α	*8*	*946.1*	*0.067*

Table B.1. Continued

	k	*AICc*	*w(AIC)*
λ(Avg surface+Avg OTM+Dist+LLd+Max surface+Woody)σ(.)α	*8*	*946.6*	*0.053*
λ(Avg OTM+%Cov+Dist+LLd+Woody)σ(.)α	*7*	*946.7*	*0.05*
λ(Avg OTM+Dist+LLd+Max surface+Woody)σ(.)α	*7*	*947*	*0.043*
λ(Avg OTM+Dist+LLd+Max OTM+Woody)σ(.)α	*7*	*947.4*	*0.036*
λ(Avg OTM+Dist+LLd+Max surface+Woody)σ(.)α	*6*	*947.5*	*0.033*
Detection Only			
λ(.)σ(Avg OTM+%Cov+Dist+Hab+Max surface+Max OTM)α	*9*	*1165.1*	*0.337*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+LLD+Max surface+Max OTM)α	*10*	*1165.9*	*0.226*

Table B.1. Continued

	k	*AICc*	*w(AIC)*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+Ma surface+Max OTM+obs)α	*13*	*1166.5*	*0.163*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+Max surface+Max OTM+Woody)α	*10*	*1167.7*	*0.089*
λ(.)σ(Avg surface+Avg OTM+%Cov+Dist+Hab+Max surface+Max OTM)α	*10*	*1169.2*	*0.043*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+Max surface+Max OTM+time)α	*11*	*1169.4*	*0.038*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+Max surface+Max OTM+obs+Woody)α	*14*	*1169.5*	*0.037*
λ(.)σ(Avg surface+Avg OTM+%Cov+Dist+Hab+LLd+Max surface+Max OTM)α	*11*	*1170.3*	*0.024*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+LLd+Max surface+Max OTM+Woody)α	*11*	*1170.4*	*0.024*
λ(.)σ(Avg OTM+%Cov+Dist+Hab+LLD+Max surface+Max OTM+time)α	*12*	*1170.8*	*0.02*

APPENDIX C

We constructed a dichotomy of criteria to gauge the exposure of *Ameiva exsul* populations to introduced mongoose. We determined the historic exposure of *Ameiva exsul* to mongoose by eliminating the possibility of current and historic distribution of mongoose in Puerto Rico. Mongoose were considered absent when none of the criteria below to indicate mongoose presence were met. We defined populations as the area of a 2 km^2 grid cell that we overlaid on the island of Puerto Rico. We followed criteria as follows:

(i) Documented occurrence of mongoose on the island?

Yes → See (ii)

No → Naïve population

(ii) PR GAP Analysis habitat suitability models for mongoose presence at sampling sites

Yes → Mongoose-exposed

No → See (iii)

(iii) CDC rabies incidence from mongoose bites in 2008 – 2014.

Yes → Mongoose-exposed

No → See (iv)

(iv) Fragmented by grasslands, pastures, shrubland. This is habitat preferred by mongoose in Puerto Rico.

Yes → Mongoose-exposed

No → See (iv)

(v) History of plantations and/or agriculture 1900 – 1950 These are potential areas for mongoose introduction.

Yes → Mongoose-exposed

No → See (vi)

(vi) Verified on the ground by talking with land owners or visual encounters

Yes → Mongoose-exposed

No → Naïve

Table C.1. We identified five mongoose-exposed and five naïve populations to sample ground lizards.

ID	Population	(i)	(ii)	(iii)	(iv)	(v)	(vi)
1	Arecibo	**Yes**	**Yes**	Yes	Yes	Yes	Yes
2	Borinquen	**Yes**	**No**	**No**	**No**	**No**	**No**
3	Caja Muertos	***No***	*Yes*	*No*	-	*No*	*No*
4	Cidra	**Yes**	**No**	**No**	**No**	**No**	**No**
5	Culebra	***No***	*Yes*	*No*	-	*Yes*	*No*
6	Culebrita	***No***	*No*	*No*	-	*No*	*No*
7	Dos Bocas	**Yes**	**Yes**	No	No	No	Yes
8	Lajas	**Yes**	**Yes**	Yes	Yes	Yes	Yes
9	Mayaguez	**Yes**	**Yes**	Yes	No	No	No
10	Vieques	**Yes**	**Yes**	Yes	Yes	Yes	Yes

Figure C.1. Environmental variables ordinated across the sites. Arrow indicates an eleventh site on St. Croix where an introduced population occurs. The first axis described a gradient of low to high precipitation. The second axis described a gradient of cool to warm sites. A Wilcoxon rank sum test found no differences in the NMDS scores between the sites with mongoose present and sites without mongoose on the first (W=16, P=0.53) or second axis (W=11, P=0.83).

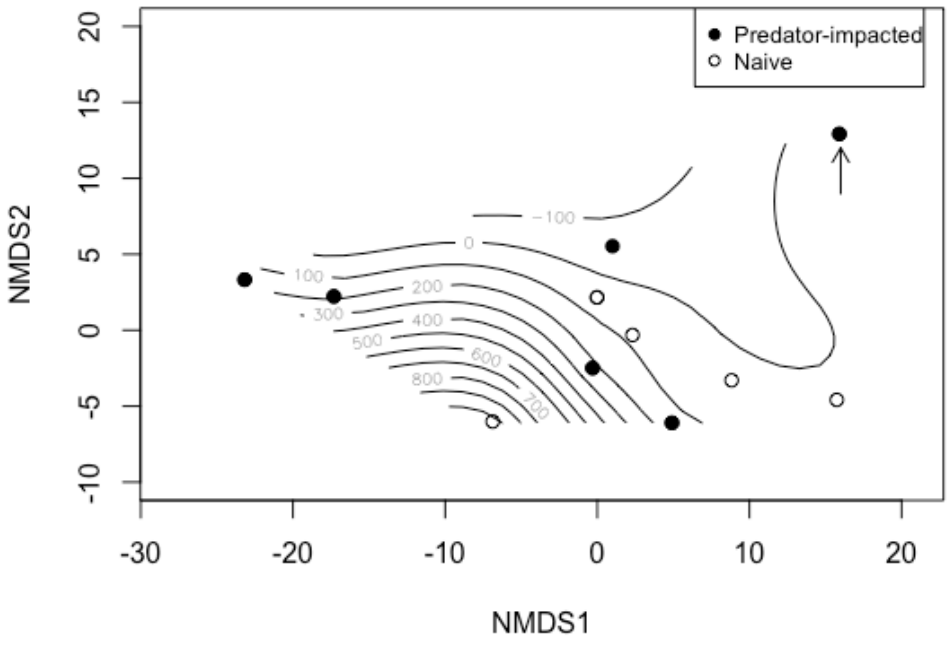


Table C.2. We identified sites to sample based on the environmental dataset a priori to sampling of the species. Data is collated from 1980 – 2010 and used by permission of the Southeast Regional Climate Center online: http://acis.sercc.com/

Station	Max Temperature (°C)	Min Temperature (°C)	Average Temperature (°C)	Heat degree days	Cool degrees days	Precipitation (mm)
Adjuntas	82.3	59.3	70.8	46	2165	73.67
Aguirre	87.7	70	78.9	0	5053	39.14
Aibonito	78.5	66	72.3	19	2682	49.76
Arecibo	88	67.9	78	0	4731	51.02
Arecibo Obs	84.9	63.5	74.3	0	3370	80.55
Barranquitas	80.4	64.5	72.5	6	2738	48.42
Borinquen	86.7	70.7	78.7	0	5000	49.07
Cayey	81.7	64.7	73.2	5	2991	56.38
Cerro Maravilla	70.9	58.7	64.9	624	576	92.71
Coloso	88.4	66	77.2	0	4461	74.27
Corozal	86.7	66.9	76.8	0	4314	72.07
Dos Bocas	87.4	67.5	77.5	0	4542	74.61
Gurabo	87.8	65.5	76.7	0	4257	62.08
Humacao	87.5	69.7	78.6	0	4952	80.4
Isabela	84.7	68.5	76.6	0	4229	62.31
Juncos	86.8	67.4	77.1	0	4416	64.77
Lajas	89	65.8	77.5	0	4537	45.01
Magueyes	89.2	72.2	80.7	0	5735	30.23
Manati	84.7	69.4	77	0	4398	56.83
Maricao	79.5	64	71.8	16	2485	95.6
Mayaguez	88.7	67.7	78.2	0	4812	68.66
Pico Del Este	69.5	60.9	65.2	475	564	169.47
Rincon	87.9	70.5	79.2	0	5176	53.8
Rio Piedras	87.2	69.7	78.5	0	4917	68.97
Roosevelt Roads	86	74.8	80.4	0	5625	52.24
San Sebastian	90.7	65.1	77.9	0	4708	90.45
SJU	85.5	74.2	79.9	0	5426	50.76
Trujillo Alto	87.7	69.5	78.7	0	4984	69.05
Utuado	86.3	63.2	74.8	0	3556	70.96

Table C.3. We identified sites to sample based on reduced dimensionality (MDS1, MDS2) of the environmental dataset a priori to sampling of the species. Data is collated from 1980 – 2010 and used by permission of the Southeast Regional Climate Center online: http://acis.sercc.com/

Station	Elevation (m)	MDS1	MDS2	Latitude (WGS 84)	Longitude (WGS 84)
Adjuntas	1830	-0.019	-0.007	18.17	-66.82
Aguirre	22.5	0.033	-0.0023	17.96	-66.22
Aibonito	2330	0.011	-0.018	18.13	-66.26
Arecibo	10	0.014	-0.002	18.45	-66.67
Arecibo Obs	1060	-0.01	0.0025	18.35	-66.75
Barranquitas	2060	0.011	-0.019	18.17	-66.32
Borinquen	218	0.019	-0.001	18.51	-67.13
Cayey	1296	0.002	-0.013	18.12	-66.17
Cerro Maravilla	4002	-0.047	-0.008	18.15	-66.56
Coloso	40	-0.00	0.006	18.38	-67.11
Corozal	650	-0.007	0.005	18.33	-66.36
Dos Bocas	200	-0.007	0.007	18.34	-66.67
Gurabo	160	0.0006	-0.001	18.26	-65.99
Humacao	131	-0.009	0.014	18.13	-65.82
Isabela	420	0.002	0.001	18.47	-67.05
Juncos	213	-0.001	0.002	18.23	-65.91
Lajas	90	0.021	-0.009	18.03	-67.07
Magueyes	12	0.051	0.003	17.97	-67.05
Manati	250	0.008	-0.001	18.43	-66.47
Maricao	2832	-0.033	0.001	18.15	-66.99
Mayaguez	74	-0.002	0.007	18.19	-67.14
Pico Del Este	3448	-0.081	-0.007	18.27	-65.76
Rincon	10	0.0142	0.002	18.34	-67.25
Rio Piedras	92	-0.00	0.0088	18.39	-66.05
Roosevelt Roads	33	0.019	0.004	18.25	-65.64
San Sebastian	194	-0.021	0.014	18.35	-67.01
SJU	9	0.021	0.002	18.43	-66.01
Trujillo Alto	115	-0.001	0.009	18.33	-66.02
Utuado	520	-0.011	0.001	18.26	-66.69

APPENDIX D

The maximum, minimum thermal critical limits, and preferred body temperatures are standard measures to determine the physiological traits of individuals across taxa (Hertz et al. 1993). At minimum body temperature, lizards lose righting response but regain homeostasis (CT_{min}), i.e., critical minimum temperature. Lizards respond to maximum body temperature with involuntary muscle contractions (onset of seizures) but regain homeostasis (CT_{max}), i.e., critical maximum temperature. The body temperature selected in a thermal gradient 20°C – 60°C (*Tpref = Tsel*) where lizards are free to thermoregulate was measured as the preferred body temperature.

Figure D.1. Physiological traits of individuals across a replicated field experiment with five populations impacted by mongoose predators (Predator-impacted) and five populations naïve to mongoose (naïve).